EARLY ANGIOSPERM DIVERSIFICATION: THE DIVERSITY OF POLLEN ASSOCIATED WITH ANGIOSPERM REPRODUCTIVE STRUCTURES IN EARLY CRETACEOUS FLORAS FROM PORTUGAL[1]

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Abstract

Studies of five mesofossil floras from the Early Cretaceous (Barremian or Aptian?) of Portugal document a previously unrecognized diversity of angiosperms exceeding that currently known from other localities of this age. At the Famalicão, Vale de Agua, and Buarcos localities angiosperms are represented by about 100 different kinds of flowers, fruits, seeds, and stamens. At the other two localities (Torres Vedras and Catefica) angiosperm diversity is lower but still significant. At each of the five localities between 7 and 26 types of angiosperm pollen have been recognized based on pollen grains in situ within anthers, or on stigmatic or fruit surfaces. Monocolpate, dicolpate, periporate, and tricolpate angiosperm pollen have been recognized, but in all cases monocolpate grains, of probable magnoliid or monocotyledonous affinity, are the most diverse element. The diversity of angiosperm pollen in situ, or associated with other angiosperm reproductive structures, is greater than that of the dispersed palynoflora from the same localities. The diversity and abundance of angiosperms in the Portuguese mesofloras contrast strongly with the apparent paucity of angiosperm pollen in dispersed palynofloras, as well as the scarcity of angiosperm wood and leaves in Barremian-Aptian fossil plant assemblages. This discrepancy may reflect the widespread occurrence of both insect pollination and herbaceous habit among the angiosperms in the initial phases of their Early Cretaceous diversification.

Numerous fossil floras of Cretaceous age that comprise three-dimensionally preserved angiosperm flowers, fruits, seeds, and dispersed stamens have been discovered within the past 15 to 20 years. These floras are particularly abundant in Upper Cretaceous sediments and have been reported from widely separate geographic regions in the Northern Hemisphere. The first comprehensive studies were based on European material, and rich Late Cretaceous floras are known from Cenomanian to Maastrichtian strata of the Czech Republic, Germany, Austria, the Netherlands, Portugal, and Sweden (Friis & Skarby, 1981, 1982; Friis, 1983, 1984; Knobloch & Mai, 1984; Friis, 1985a, b; Knobloch & Mai, 1986; Friis et al., 1988; Friis & Crane, 1989; Friis, 1990; Knobloch & Mai, 1991; Friis et al., 1992; Eklund et al., 1997; Eklund & Kvaček, 1998). In North America, similarly rich Late Cretaceous floras are known from Cenomanian to Campanian strata of Massachusetts, Maryland, New Jersey, North Carolina, and Georgia (Friis, 1988; Friis et al., 1988; Drinnan et al., 1990, 1991; Herendeen, 1991; Herendeen et al., 1993; Nixon & Crepet, 1993; Crepet & Nixon, 1994; Herendeen et al., 1994; Crane & Herendeen, 1996; Frumin & Friis, 1996; Magallón-Puebla et al., 1996, 1997). In Asia, fossil flowers and fruits have been reported from Coniacian to Campanian strata of Japan (e.g., Nishida & Nishida, 1988; Nishida, 1994; Nishida et al., 1996) and have recently been discovered from Cenomanian-Turonian strata of Kazakhstan (Frumin & Friis, 1996, 1999). The angiosperms recovered in

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these Late Cretaceous floras exhibit great taxonomic diversity and document the presence of many major angiosperm lineages at the ordinal and family level (Magallón-Puebla et al., 1999, this issue).

From the Early Cretaceous, well-preserved floras with flowers, fruits, seeds, and stamens are known from North America (the Potomac Group sequence) and from Portugal. From the Potomac Group, the best preserved and most diverse floras are from the late Aptian-Albian (Friis et al., 1986, 1988; Drinnan et al., 1991; Crane et al., 1994; Friis et al., 1994a; Pedersen et al., 1994b; Friis et al., 1995; Crane & Herendeen, 1996; Friis et al., 1997a). From Portugal, rich floras with angiosperm reproductive organs have been discovered in the Western Portuguese Basin, and the most important localities are in the area around Torres Vedras and the Runa Basin, the vicinity of Cós-Juncal-Leiria, and the area around Buarcos-Tavarede (Friis et al., 1994b; Pedersen et al., 1994a; Friis et al., 1997a, b). The Portuguese floras are thought to be of Barremian or possibly Aptian age and contain the most diverse assemblages of early angiosperms currently known.

The earliest angiosperm remains that can be recognized reliably in the fossil record are dispersed pollen grains in palynofloras of Early Cretaceous age (Valanginian-Hauterivian). In these earliest Cretaceous palynofloras angiosperm pollen is rare but occurs over a large area that includes Israel, Italy, and southern England. From the Valanginian of Italy monoaperturate angiosperm pollen with reticulate-columellate wall structure was reported but not illustrated from a sequence dated partly by marine dinoflagellate cysts (Trevisan, 1988). Trevisan (1988) noted considerable morphological diversity among these Valanginian grains. Angiosperm pollen is also present, but extremely rare, in late Valanginian to early Hauterivian strata of Israel where it comprises less than 2‰ of the total palynomorph assemblage (Brenner, 1984; Brenner & Bickoff, 1992; Brenner, 1996). In palynofloras from the Hauterivian of southern England, angiosperm pollen grains are also rare but show a considerable diversity in the form of the reticulum and the ornamentation of the tectum. Hughes (1994) illustrated more than 10 different dispersed monoaperturate pollen taxa from this time interval, each typically represented by a few specimens only. In Barremian and younger palynofloras there is a marked increase in diversity and abundance of dispersed angiosperm pollen, and tricolpate pollen is first reported from this time interval.

In this paper we discuss the angiosperm component of five Early Cretaceous (Barremian or Aptian?) fossil floras from Portugal that contain flowers, fruits, seeds, and stamens. We focus particularly on documenting the diversity of angiosperm pollen grains found in situ in stamens, within flowers adhering to the stigmatic or fruit surfaces of carpels, or on dispersed fruits. We show that the diversity of fossil pollen assessed in this way is higher than the diversity of angiosperm pollen taxa currently recognized in mid-Cretaceous dispersed palynofloras.

Material and Methods

The five floras discussed in this work include the Torres Vedras flora (northeast of Forte da Forca), the Catefica flora, the Vale de Agua flora, the Famalicão flora, and the Buarcos flora. The effort expended so far in studying each of these floras is about equivalent and therefore the quantitative estimates of their composition provided below are broadly comparable.

The Torres Vedras flora was collected in 1989 (KRP, EMF, PRC) and in 1990, 1992, 1994, and 1995 (KRP, EMF) from a large clay pit northeast of Torres Vedras, about 1 km northeast of Forte da Forca on the road toward Sarge (39°06′13″N, 9°14′47″W, Carta Geológica de Portugal Torres Vedras 30C, Zbyszewski et al., 1955). The sediments exposed in the clay pit include light yellowish and purple silts and clays, as well as grayish clays, silts, and sands with horizons of coalified material. The angiosperm component is less diverse in the Torres Vedras flora than in the other Portuguese floras, but some samples are distinctive in containing many angiosperm stamens.

The Catefica flora was collected in 1989 (KRP, EMF, PRC) and in 1992, 1994, and 1995 (KRP, EMF) in a road cut close to the village of Catefica, about 4 km south of Torres Vedras (39°3′30″N, 9°14′30″W, Carta Geológica de Portugal 30-D Alenquer, Zbyszewski & Torre de Assunção, 1965). The Cretaceous strata at Catefica are deposited close to the western margin of the Runa Basin (cf. Rey, 1972) and consist of crossbedded sands with intercalated clay beds and darker organic-rich horizons. The fossil flora extracted from these fluviatile sediments comprises several angiosperm flowers, fruits, and seeds as well as stamens with pollen in situ, cheirolepidiaceous twigs (*Pseudofrenelopsis* Nathorst), a variety of ferns, selaginellaceous shoots, and numerous fragments of thalloid liverworts.

The Vale de Agua flora was collected in 1989 (KRP, EMF, PRC), in 1992 and 1994 (KRP, EMF), and in 1997 (KRP) in a large complex of clay pits close to the small village of Vale de Agua, and

about 5 km southwest of Batalha (39°37′15″N, 8°51′30″W, Carta Geológica de Portugal 27-A Vila Nova de Ourém, Zbyszewski et al., 1974). The sediments are predominantly gray, reddish, or greenish clays belonging to the "Complexos gresosos de Nazaré e de Cós-Juncal." The flora includes numerous angiosperm flowers, fruits, seeds, and dispersed stamens, as well as many twigs and cones of cheirolepidiaceous plants. In situ angiosperm pollen grains have been observed in many of the flowers and dispersed stamens.

The Famalicão flora was collected in 1989 (KRP, EMF, PRC) in the outskirts of the small village of Famalicão, about 5 km SSE of Leiria (39°42′16″N, 8°46′12″W, Carta Geológica de Portugal 23-C Leiria, Teixeira et al., 1968). The plant-bearing horizon was a thin gray and organic-rich clay discovered in the basal part of the pit. The deeper part of the clay pit is now infilled, and the plant-bearing horizon no longer accessible for collecting. The flora includes diverse and numerous angiosperm flowers, fruits, and seeds, as well as some dispersed stamens. Compared to the other Portuguese floras, remains of cheirolepidiaceous plants are rare.

The Buarcos flora was collected in 1992, 1994, and 1995 (KRP, EMF) in the town of Buarcos north of Figueira da Foz (40°09′54″N, 8°52′11″W, Carta Geológica de Portugal 19C Figueira da Foz, Rocha et al., 1981). The plant-bearing sediments are coarse, crossbedded sands with intercalated layers of silt and clay and belong to the "Arenitos de Carrascal" complex. The flora includes a rich assemblage of angiosperm flowers, fruits, seeds, and anthers, as well as many twigs of cheirolepidiaceous plants. Palynological analysis of a clay sample from the same exposure tentatively indicated a Barremian-Aptian age (Pais & Reyre, 1981). The rich Early Cretaceous leaf flora of Buarcos described by Saporta (1894) and Teixeira (1948) was collected at another site and is perhaps not contemporaneous with the mesoflora described here. The leaf flora contains a diversity of angiosperm leaves in addition to ferns and conifers and is one of the richest angiosperm macrofloras from the Early Cretaceous.

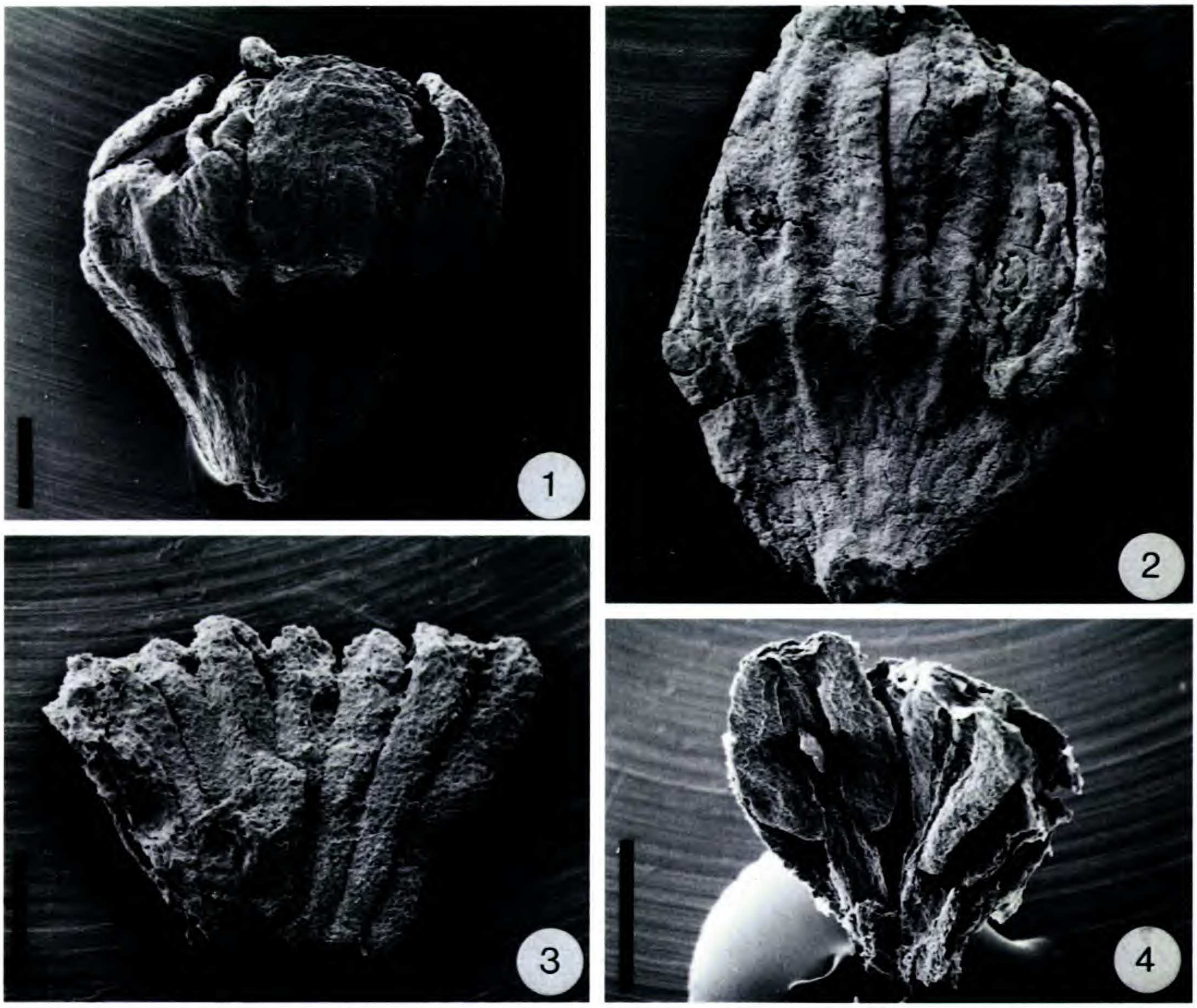
The five mesofloras have many taxa in common indicating that they are probably more or less contemporaneous, and in all cases the fossils occur in terrestrial sediments of lacustrine or fluviatile origin. Marine control is generally absent and the dating of these terrestrial plant assemblages is problematic, but the age of the five mesofossil floras considered here is thought to be Barremian or possibly Aptian (Friis et al., 1997a). Detailed geological mapping is available for the Estremadura region including the Torres Vedras-Runa area (Rey, 1972, 1979, 1982). According to Rey (1972), the strata northeast of Forte da Forca that yield the Torres Vedras flora are Valanginian to early Barremian in age (Valanginian-Hauterivian at the collection site for the Torres Vedras flora). No Aptian strata were indicated for this area. The strata south of Catefica, where the Catefica flora was collected, are Hauterivian-early Barremian (Rey, 1972). The presence of several different types of tricolpate pollen in the Torres Vedras flora and in some of the other floras may indicate a slightly younger age than is suggested by the geological data, but tricolpate pollen grains are known from Barremian strata in England (Hughes & McDougall, 1990; Penny, 1991), and it is possible that the tricolpate grains in the Portuguese floras are also pre-Aptian. Palynological analyses of samples from the Buarcos site tentatively indicate a Barremian-Aptian age (Pais & Reyre, 1981). Most of the in situ pollen discovered in the Portuguese floras are monoaperturate, and many are comparable to forms reported from the Hauterivian, Barremian, or Aptian, and sometimes also from the Albian and Cenomanian in other areas, but there are also many angiosperm pollen types that apparently have not been described from dispersed palynofloras.

The fossil fruits, seeds, and stamens in all five floras are typically preserved as three-dimensional charcoal fossils or as slightly compressed lignite fossils. They were extracted from the sediment samples and prepared for scanning and transmission electron microscopy (SEM and TEM) using standard methods as described by Friis et al. (1988). The specimens were studied using a Philips SEM 515 scanning electron microscope and a Jeol-100S transmission electron microscope. Specimens described in this work are stored in the Palaeobotanical Department of the Swedish Museum of Natural History, Stockholm (S).

Results

Diversity in Reproductive Organs

Among the five Early Cretaceous assemblages discussed here the angiosperm component of the Famalicão flora is by far the most diverse and includes many thousands of specimens representing at least 105 different types of angiosperm flowers, fruits, and seeds. Pollen grains occur in situ in flowers and dispersed stamens, and also adhering to the carpels. So far, 13 different angiosperm pollen types have been recognized. Associated with the angiosperm reproductive organs are about 15 different types of gymnospermous seed, which are probably of cheirolepidiaceous and gnetalean affin-



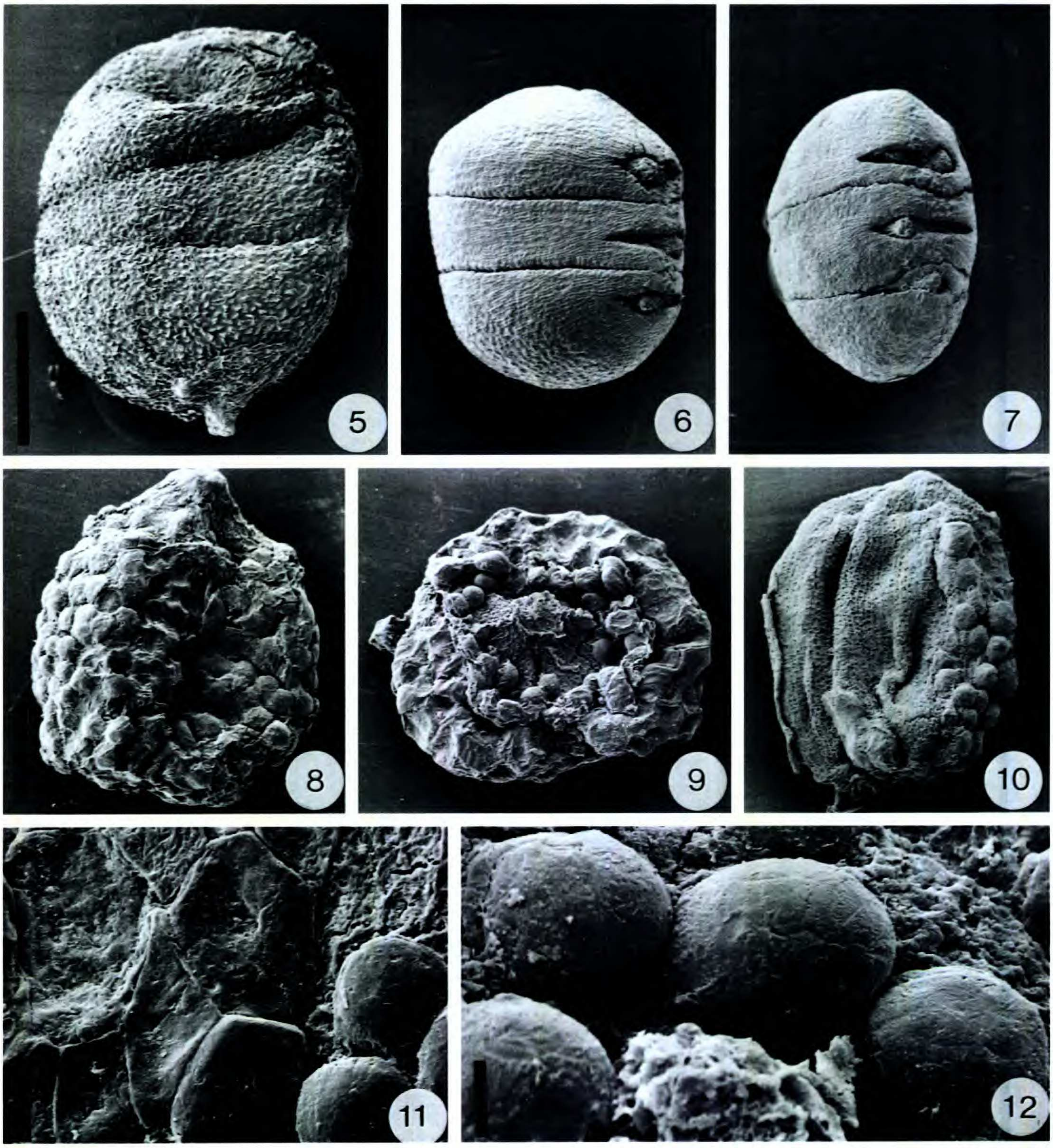
Figures 1–4. Scanning electron micrographs of angiosperm flowers and stamens from the Early Cretaceous (Barremian or Aptian?) of western Portugal. —1. Epigynous flower from the Catefica flora (sample 49), S100757, ×40; scale equal to 250 μm. —2. Epigynous flower from the Famalicão flora (sample 25), S105906, ×40; scale shown in Figure 1. —3. Several stamens from a possible chloranthaceous staminate inflorescence from the Torres Vedras flora (sample 44), S105015, ×60; scale equal to 250 μm. —4. Fragment of a small flower with two complete stamens from the Buarcos flora (sample 209), S101739, ×70; scale equal to 250 μm.

ity. The sample also contains many twigs of cheirolepidiaceous plants. All stamens and anthers discovered so far in the Famalicão flora, and many of the flowers, fruits, and seeds, have been studied preliminarily using SEM. However, there are still many taxa that have not been studied in detail, and it is likely that the diversity of angiosperm reproductive organs and pollen in situ will increase as our studies progress.

The fossil floras from Vale de Agua, Catefica, and Torres Vedras are less diverse than that from Famalicão, and most of the angiosperm flowers, fruits, and seeds recorded are also present in the Famalicão flora. The Buarcos flora also shares many taxa with that from Famalicão, but it is distinct from the other four fossil assemblages in having a higher percentage of unique taxa.

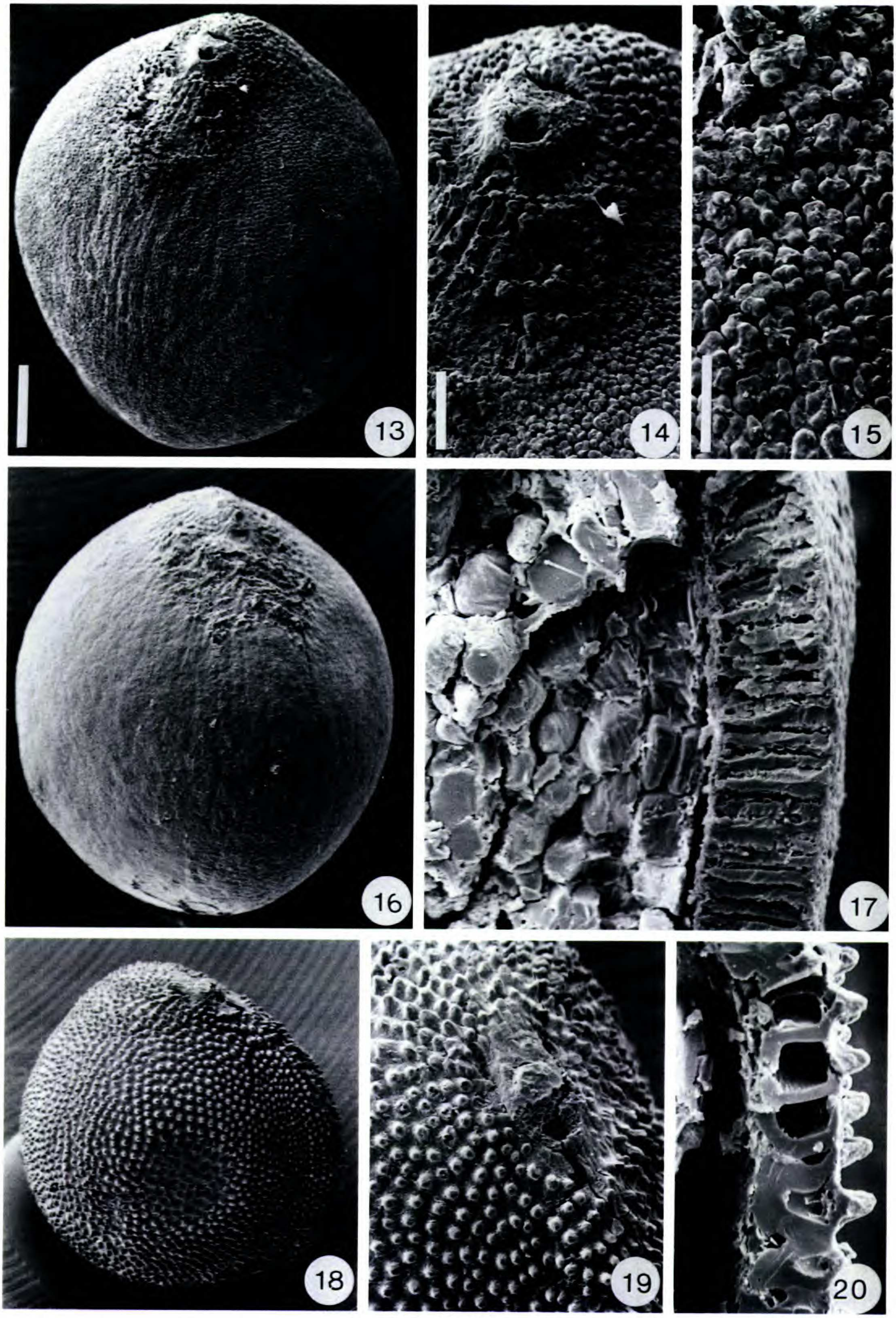
All of the angiosperm taxa represented by reproductive organs, and probably most of the non-angiospermous seed-plant taxa recorded in the Portuguese floras, appear to be new to science, and formal descriptions and comparison with extant angiosperms are still in progress. The angiosperm component in the floras consists mostly of fruits and seeds, but there are also several flowers and dispersed stamens. Some of this material has been figured in previous studies (Friis et al., 1994b, 1997a, b). Our main focus here is on the diversity of pollen in situ, but we also illustrate a small selection of flowers, fruits, and seeds that have not been published previously to indicate the quality of preservation and diversity of the angiosperm reproductive structures in these assemblages (Figs. 1–29).

Flowers. Many of the taxa in the Portuguese floras show character combinations that indicate a



Figures 5–12. Scanning electron micrographs of angiosperm fruits and seeds from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 5–7. Fruit with tightly co-adhering exotestal seeds. —5. Fruit showing thin fruit wall and several seeds, S105130, ×35; scale equal to 500 μm. —6. Oblique lateral view of three co-adhering seeds from a single fruit, S105154, ×35; scale shown in Figure 5. —7. Apical view of three co-adhering seeds from a single fruit showing slit in outer integument and projecting inner integument that forms the micropyle, S105155, ×35; scale shown in Figure 5. 8–12. Fruit with abundant resin bodies in the fruit wall. —8. Lateral view of fruit showing thin fruit wall and prominent resin bodies, S105187, ×50; scale equal to 250 μm. —9. Apical view of fruit showing stigmatic area, S105184, ×50; scale shown in Figure 8. —10. Fruit with most of fruit wall and resin bodies abraded showing two seeds, S105191, ×50; scale shown in Figure 8. —11, 12. Details of fruit wall showing polygonal epidermal cells and spherical resin bodies in fruit wall. 11: S105188, ×250; scale equal to 40 μm.; 12: S105186, ×400; scale equal to 25 μm.

magnoliid or perhaps monocotyledonous affinity. There are several distinct flower types in the Portuguese floras (Friis et al., 1994b). Some are represented by a single specimen, others are more abundant and occur in more than one flora. One of the more abundant types includes small epigynous, bisexual flowers with one whorl of triangular leathery tepals and perhaps two whorls of stout stamens (Figs. 1, 2; flowers with pollen types A.1 and A.2, Figs. 30–38). The stamens have anthers with val-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vate dehiscence and a distinct apical protrusion of the connective. The number of parts is apparently variable with five to seven parts in each whorl. The gynoecium is bicarpellate, but usually only a single seed is developed. At least two different species are present and are distinguished mainly based on differences in size and shape of tepals, stamens, and ovary. Pollen grains have been found in situ in both species and have a characteristic finely striate tectum ornamentation that forms a fingerprint-like pattern (pollen types A.1 and A.2, Figs. 30–38). The pollen from the two different species differs in aperture configuration and fine details of the ornamentation, with monocolpate and trichotomocolpate grains in one species and dicolpate grains in the other. Extant *Cabomba* Aubl. has similar striate pollen, but the fossil flowers are distinct from those of *Cabomba* or other members of the Cabombaceae, which all have trimerous, hypogynous flowers. Trichotomocolpate and dicolpate aperture configuration has not been reported for pollen of extant *Cabomba*, but it does occur in several monocotyledons, and in the magnoliid family Hydnoraceae.

Another common flower in the Portuguese fossil floras is a minute epigynous, pistillate form closely related to the extant Chloranthaceae genus *Hedyosmum* Sw. Such flowers are known from all five of the Portuguese floras (flower with pollen type J.7, Figs. 114–116). They are extremely simple, consisting of three tepal-like structures at the apex of a unilocular and uniovulate ovary. The flower has a characteristic opening in the hypanthium wall, the so-called "window" (Friis et al., 1997b). Pollen grains attached to the surface of the female flowers are of the *Asteropollis*-type, a dispersed pollen genus that is closely similar to pollen of extant *Hedyosmum* (e.g., Walker & Walker, 1984). Pollen is monoaperturate with a star-shaped aperture and a reticulate tectum with muri that have a characteristic beaded ornamentation. *Asteropollis*-type pollen similar to that observed on the fruits has also been found in situ in stamens from the Portuguese floras, and a variety of other pollen types (pollen types J.1–12, Figs. 97–121) resembling pollen of extant *Hedyosmum* and *Ascarina* J. R. & G. Forst. have been found in dispersed stamens or fragments of staminate inflorescences (e.g., Fig. 3 with pollen type J.2, Figs. 100–102). Several have distinct trichotomocolpate apertures.

Among the hypogynous floral structures from the Portuguese localities is a small flower with a trimerous androecium and gynoecium (flower with pollen type D.5, Figs. 61–63). Pollen in situ within the stamens is small, monocolpate, and reticulate. The flower was previously described as "epigynous (?) flower with reticulate pollen" by Friis et al. (1994b), but removal of the perianth has now demonstrated that the flower is hypogynous. The androecium is incomplete, but the position of the stamens that are preserved shows that the flower originally had nine stamens. The base of the flower is broken, and it is not possible to establish whether the stamens are in one or several whorls. Each stamen consists of a broad filament bearing a tetrasporangiate anther, about 0.6 mm long. The gynoecium consists of three carpels. The number of perianth parts and their organization are unclear. The systematic affinity of the flower remains to be established, but the trimerous arrangement of the androecium and gynoecium combined with the monocolpate pollen may indicate a monocotyledonous affinity. A reticulum supported by densely spaced columellae is also common among many extant monocotyledons, e.g., some Agavaceae and palms (Alvarez & Köhler, 1987; Harley, 1997).

Another small hypogynous flower is represented by a single, fragmentary specimen (Fig. 4; flower with pollen type B.4, Figs. 47–49). It consists of an outer whorl of membranous tepals and an inner whorl of stamens. Stamens and tepals are of about the same length, and stamens consist of a distinct filament bearing a tetrasporangiate anther with valvate dehiscence. Two tepals and two complete stamens as well as a fragment of a third stamen are present, but the specimen is incompletely preserved, and the original number of parts is un-

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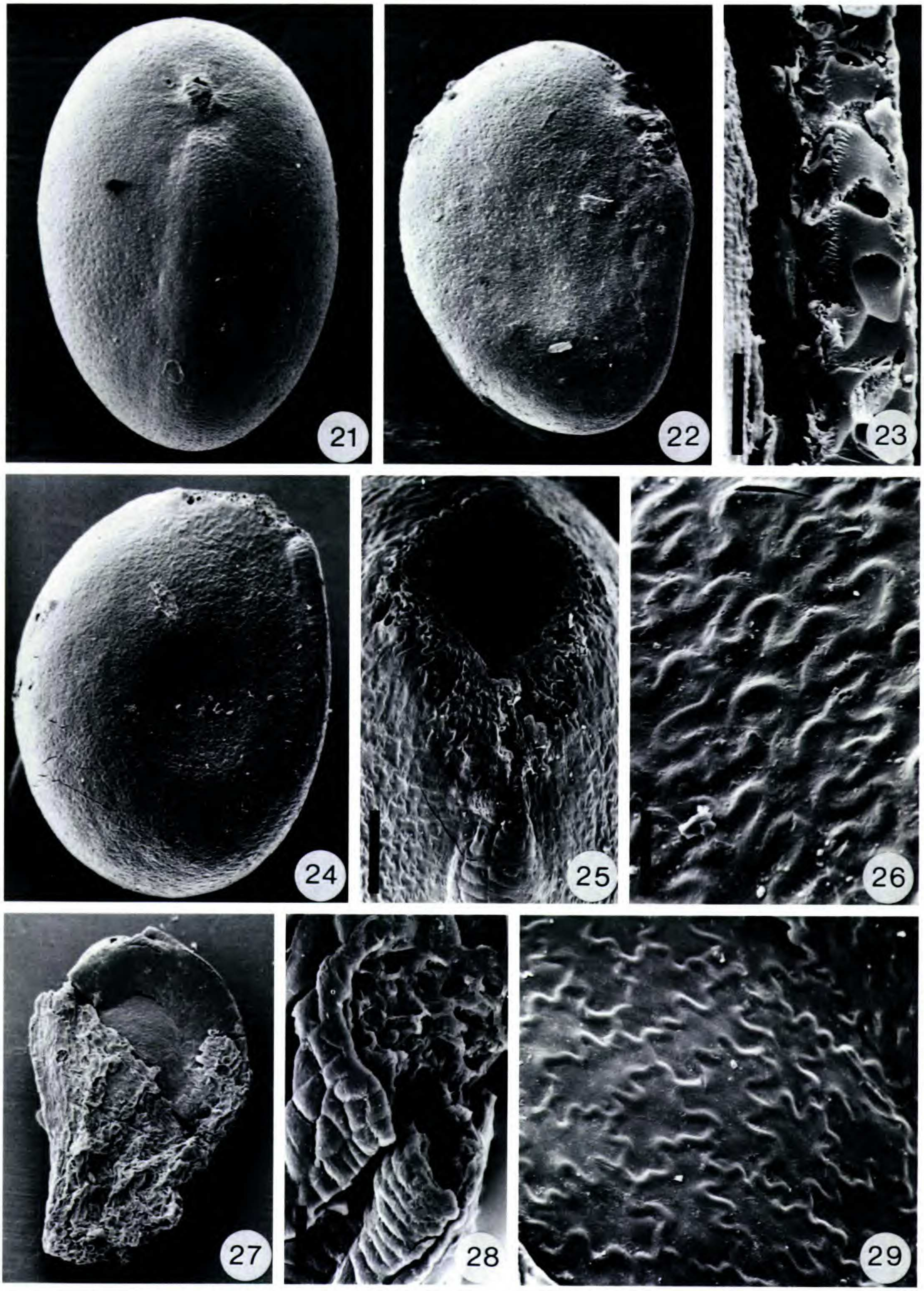
Figures 13–20. Scanning electron micrographs of exotestal angiosperm seeds from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 13–15. Exotestal seed with slightly verrucate surface. —13. Oblique dorsiventral view showing seed and micropylar area, S105221, ×50; scale equal to 250 μm. —14. Detail of micropylar area enlarged, S105221, ×120; scale equal to 100 μm. —15. Detail of seed surface showing verrucate ornamentation, S105221, ×300; scale equal to 50 μm. 16, 17. Exotestal seed with almost smooth surface and narrow, high palisade cells. —16. Dorsiventral view of seed and micropylar area, S105224, ×50; scale shown in Figure 13. —17. Detail of seed wall showing palisade cells of exotesta, S105223, ×300; scale shown in Figure 15. 18–20. Exotestal seed with fine spines and short palisade cells. —18. Lateral view of seed, S105225, ×50; scale shown in Figure 13. —19. Detail of seed showing micropylar area, S105225, ×120; scale shown in Figure 14. —20. Detail of seed wall showing outer short palisade cells of testa and spiny surface of seed, S105228, ×300; scale shown in Figure 15.



Figures 21–29. Scanning electron micrographs of angiosperm seed with exotestal seeds and digitate anticlinal cells from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 21–23. Seed type with digitate palisade cells over raphe. —21. Dorsiventral view of seed and raphe, S105218, ×50; scale equal to 250 μm. —22. Lateral view of seed, S105220, ×50; scale shown in Figure 21. —23. Detail of palisade cells, S105219, ×600; scale equal to 25 μm. 24–26. Seed type with non-digitate cells over raphe, S105027. —24. Lateral view, ×50;

known. The pollen grains are monoaperturate, with both monocolpate and trichotomocolpate pollen produced by the same anther. The graded (*Similipollis*-type) tectum of the pollen wall from psilate to reticulate indicates a possible relationship with the monocotyledons, but the systematic affinity of the fossil flower cannot be established based on our current knowledge of the floral structure.

Fruiting units. There are many unilocular fruiting units, some of which may be from unicarpellate gynoecia, while others may be dispersed fruitlets from apocarpous, multicarpellate structures. Usually there are only one, or a few, seeds per carpel, and the stigmatic area is sessile (Figs. 5–10). One type of fruiting unit that occurs abundantly in the Portuguese floras belongs to the extinct genus *Anacostia* Friis, Crane & Pedersen, which is based on unicarpellate, apparently baccate, fruiting units with a single anatropous, bitegmic, and exotestal seed (Friis et al., 1997a). The stigmatic area is indistinct and sessile. Monoaperturate (monocolpate and trichotomocolpate) pollen grains with a characteristic graded reticulum have been observed on many specimens (see description of pollen type F). The fruit wall contains scattered resin bodies, thought to represent the remains of ethereal oil cells. Fruit characters indicate a possible magnoliid affinity, while pollen features indicate a possible affinity to monocotyledons. In the Portuguese floras two species have been distinguished: *Anacostia portugallica* Friis, Crane & Pedersen described from Vale de Agua, Famalicão, and Buarcos, and *A. teixeirae* Friis, Crane & Pedersen described from Famalicão and Buarcos (Friis et al., 1997a). Two other species of *Anacostia* were described from the Early Cretaceous of North America (Friis et al., 1997a). Other unilocular and one-seeded fruiting units in the Portuguese floras are related to the extinct genera *Couperites* Pedersen, Crane, Drinnan & Friis and *Appomattoxia* Friis, Pedersen & Crane, described earlier from mid-Cretaceous strata of North America (Pedersen et al., 1991; Friis et al., 1995).

Like *Anacostia* several of the angiosperm fossils in the Portuguese Early Cretaceous floras have resin bodies that probably represent the remains of ethereal oil cells. This feature is characteristic for many extant magnoliids, and among the monocotyledons is only reported from the genus *Acorus* L. One resinous fruit type that has been reported from all floras studied is particularly abundant in the Famalicão flora (Figs. 8–12). The material is thought to include two different species of the same genus. Resin bodies are densely spaced under the cuticle of the fruit wall. Each fruit includes two anatropous and apparently endotestal seeds with a small, subbasal heteropyle. The seed wall has an endotestal tissue with distinct crystal cells. The seeds are very similar to those of *Liriodendron* L. and other Magnoliaceae in organization and wall structure. Pollen grains are found in large quantities on the surface of the fruit, particularly in the stigmatic area. They are monoaperturate with a loose, coarse reticulum and long columellae (see described pollen type D.9, Figs. 72–74). They are unlike pollen of extant Magnoliaceae, and the fossil may belong to an extinct group of magnoliids.

Seeds. Both endotestal and exotestal angiosperm seeds occur in the Portuguese fossil floras, but exotestal seeds are especially abundant and diverse (Figs. 13–29). These seeds have the mechanical layer in the outer seed wall, and the outer epidermis is often developed as a palisade layer. Frequently, they can be recognized in fossil assemblages as black, shiny objects. They are all anatropous and vary in size, shape, and testa ornamentation, as well as in anatomical details. Some of them show similarities to seeds of extant Nymphaeales in having distinctly digitate anticlinal cell walls of the outer palisade layer (Figs. 21–29), but only one (not figured here) has the characteristic micropylar lid of the Nymphaeales and their relationships may be to other magnoliids, or some may be on the Nymphaeales stem lineage. Exotestal seeds with palisade cells and digitate cell wall occur also in the Illiciales, and it is possible that some of the Early Cretaceous angiosperm seeds from Portugal are related to this group. Seeds with unequivocal features of Illiciaceae have been documented from younger (Cenomanian-Turonian) strata of Kazakhstan (Frumin & Friis, 1999).

A distinctive exotestal seed type encountered in all five fossil floras is particularly abundant at Famalicão. Several thousand specimens have been isolated (Figs. 6, 7). Several different species per-

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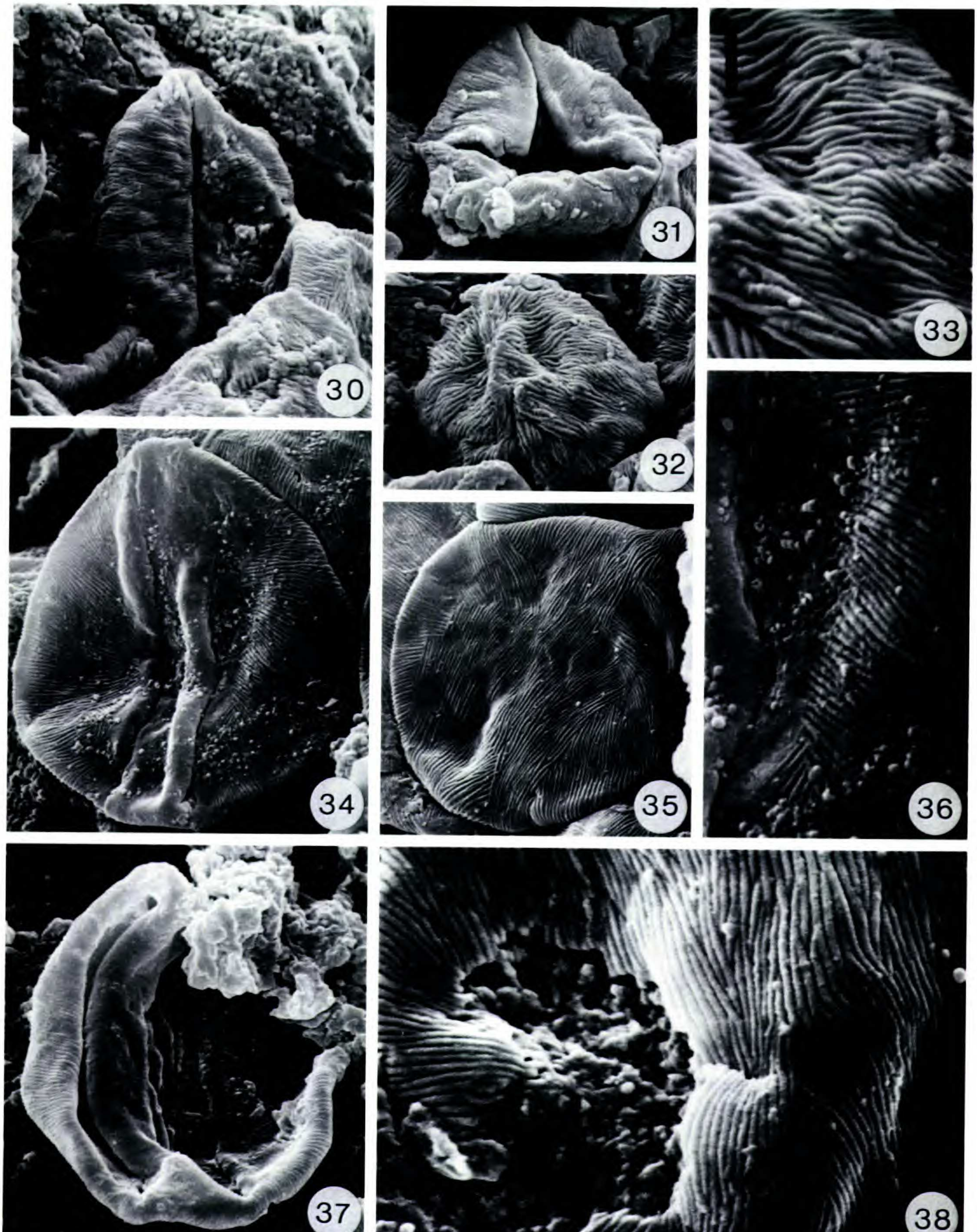
scale shown in Figure 21. —25. Detail of micropylar area, ×120; scale equal to 100 μm. —26. Detail of external surface showing digitate outlines of the palisade cells, ×500; scale equal to 25 μm. 27–29. Thin-walled seed in unilocular fruit, S105096. —27. Lateral view of seed surrounded by fragmentary fruit wall, ×50; scale shown in Figure 21. —28. Detail of micropylar area, ×400; scale equal to 25 μm. —29. Detail of external surface showing digitate outlines of the palisade cells, ×400; scale shown in Figure 28.



Figures 30–38. Scanning electron micrographs of pollen type A from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 30–33. Pollen type A.1, monocolpate-trichotomocolpate, finely striate pollen, S105030 (Vale de Agua sample 19). —30. Distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —31. Distal view showing trichotomocolpate aperture, ×4000; scale shown in Figure 30. —32. Proximal view showing fingerprint-like striations, ×4000; scale shown in Figure 30. —33. Detail of finely striate exine, ×10,000; scale equal to 1 μm. 34–38. Pollen type A.2, dicolpate, tectate, finely striate pollen, S101288 (Vale de Agua sample 141). —34. Distal view showing two colpi, ×4000; scale shown in Figure 30. —35. Proximal view showing finely striate exine, ×4000; scale shown in Figure 30. —36. Detail of finely striate exine, ×10,000; scale shown in Figure 33. —37. Distal view showing two colpi, ×4000; scale shown in Figure 30. —38. Detail of finely striate exine showing apparently granular infratectal structure where the surface is broken, ×10,000; scale shown in Figure 33.

haps belonging to different genera have been recognized. One species has one to six seeds per carpel, the most common number being three seeds (Figs. 6, 7). The seeds are anatropous and bitegmic and laterally co-adhering to each other. The micropyle is formed by the thin inner integument, while the outer integument forms an elongated slit around it. The seeds occur in unilocular fruits (Fig. 5) with a thin fruit wall without mechanical tissue. The fruit wall was perhaps originally fleshy and is mostly abraded. The stigma is indistinct and sessile. No pollen grains have been observed on the stigmatic area, although numerous specimens have been examined. The second, presumably closely related species, differs in having larger and more elongated seeds. A third species typically has four laterally fused seeds per carpel, and the fruits are of more regular, almost spherical shape.

DIVERSITY OF IN SITU POLLEN

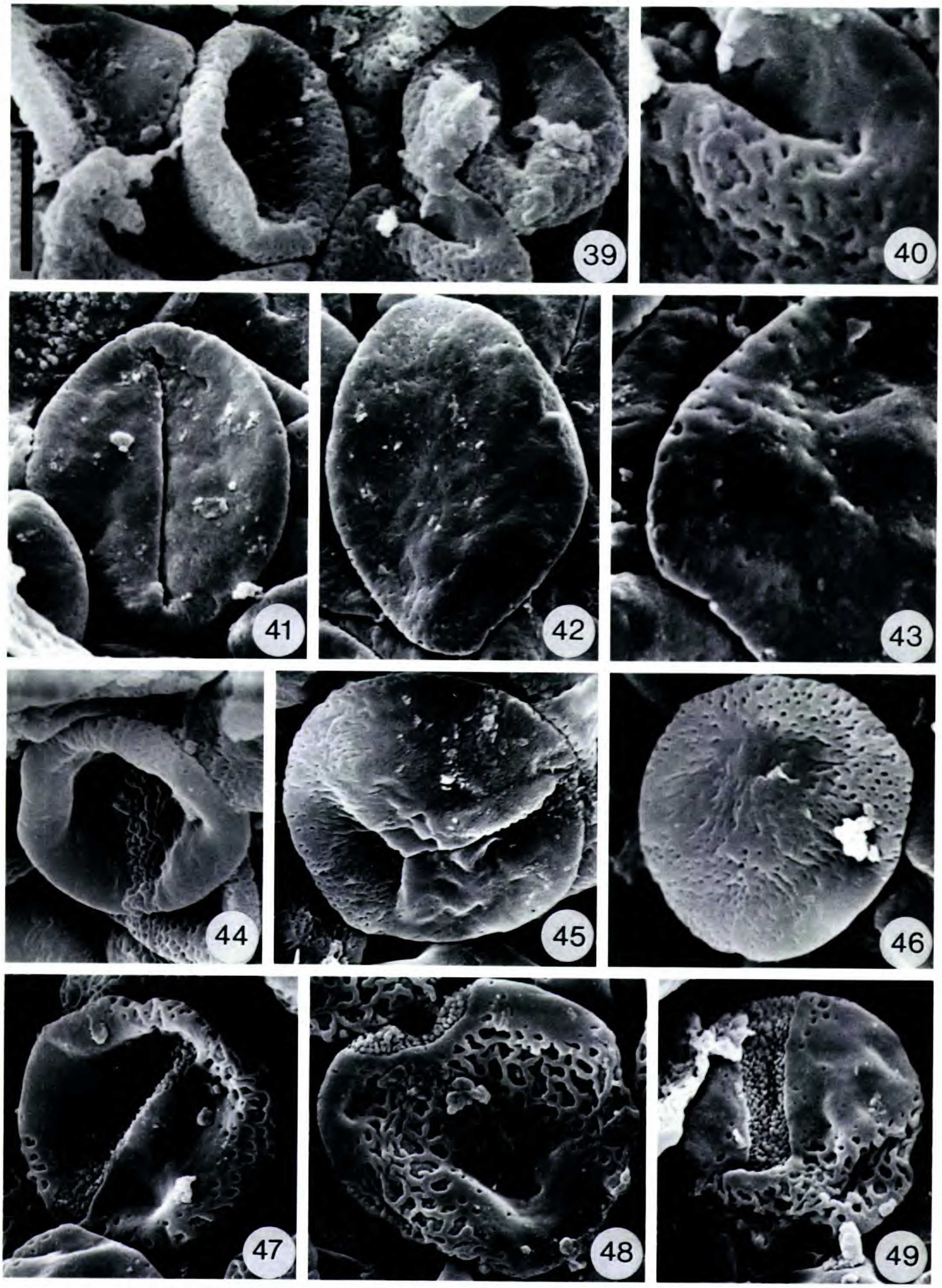
In all five of the Portuguese floras discussed here pollen grains have been found in situ in flowers or dispersed stamens or on the surface of dispersed fruits. Several of these pollen grains are closely similar to pollen described from dispersed palynofloras, but detailed comparisons are often problematic because the dispersed pollen species are usually characterized based only on light microscopy (LM). Light microscopy does not provide sufficient information on ornamentation and other fine details that are readily observed by the SEM and that are of clear taxonomic importance. For example, studies of an assemblage of minute, monocolpate, and finely reticulate angiosperm pollen grains from the Barremian of southern England based on LM studies resulted in the recognition of only a single species, *Clavatipollenites hughesii* Couper, while details retrieved by SEM demonstrated that this assemblage included ten or more distinct species (e.g., Hughes et al., 1979; Hughes, 1994). A similar example was discussed by Penny (1988) based on SEM studies of an extensive collection of semitectate-acolumellate pollen grains from the Early Cretaceous of Egypt. Other SEM-based palynological studies show similar results with higher diversity of pollen taxa than retrieved by LM studies from comparable samples.

About 60 different pollen types have been found in situ from the five Portuguese Early Cretaceous floras. Monoaperturate, dicolpate, and periporate pollen grains of probable magnoliid and monocotyledonous affinity are by far the most diverse with 48 different taxa identified so far of which 44 are described here. About 10 different tricolpate pollen types of presumed eudicotyledons have been observed. All of the early angiosperm pollen grains described here are small, ranging from about 9 to 25 μm in their maximum diameter. Only one pollen type is larger than 30 μm, and most are in the size range of 12–16 μm. Semitectate and reticulate forms predominate and comprise about 75% of the pollen types recognized so far. The remainder are tectate-foveolate or tectate-striate. Trichotomo-, tetrachotomo-, and pentachotomocolpate apertures are common. In two different species monocolpate and trichotomocolpate grains were observed in situ in the same anther. Pollen grains associated with the fruits of *Anacostia* also include both monocolpate and trichotomocolpate forms (Friis et al., 1997a).

In this study we concentrate on the diversity of probable magnoliid and monocotyledonous pollen, providing brief descriptions, comments on their occurrence in the five Portuguese floras, and a brief consideration of the type of organ with which they are associated. The pollen grains are grouped according to their morphological features. They are not referred to genera or species based on dispersed grains, although possible links to dispersed taxa are discussed when relevant.

A. Monocolpate-trichotomocolpate and dicolpate, tectate and finely striate pollen (Figs. 30–38). Two very similar tectate and finely striate pollen species have been identified. Both are found in situ in small epigynous flowers with a distinct perianth of leathery tepals (Figs. 1, 2). These flowers occur in the Catefica, Vale de Agua, Buarcos, and Famalicão floras, and their systematic position remains to be investigated in detail.

The pollen grains are similar to pollen of extant *Cabomba* (Cabombaceae, Nymphaeales) in wall ornamentation, but dicolpate or trichotomocolpate apertures have not been observed in pollen of Cabombaceae, and the epigynous organization of the flowers, as well as number of floral parts, precludes an affinity with members of this family. Dicolpate pollen with two closely spaced (distal) colpi and monocolpate/trichotomocolpate pollen is common among monocotyledons and is also known for the magnoliid family Hydnoraceae. We have not seen similar tectate-striate pollen grains reported from dispersed Early Cretaceous palynofloras. The two species of pollen are distinguished from each other in size, aperture configuration, and details of ornamentation. Despite these differences they are thought to be closely related. They occur in very similar flowers and both have the characteristic striate ornamentation.



Figures 39–49. Scanning electron micrographs of pollen type B from the Early Cretaceous (Barremian or Aptian?) Vale de Agua, Buarcos, and Torres Vedras floras, western Portugal. 39, 40. Pollen type B.1, monocolpate, psilate-foveolate pollen, S105257 (Vale de Agua sample 141). —39. Several pollen grains; grain at right in distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —40. Detail of exine at the equatorial region, ×10,000; scale equal to 1 μm. 41–43. Pollen type B.2, monocolpate, psilate-finely foveolate pollen, S105024 (Buarcos sample 243). —41. Distal view showing monocolpate aperture, ×4000; scale shown in Figure 39. —42. Proximal view, ×4000; scale shown in Figure 39. —43. Detail of exine in equatorial region, ×10,000; scale shown in Figure 40. 44–46. Pollen

A.1. Monocolpate-trichotomocolpate pollen (Figs. 30–33). Pollen grains small, elliptical to circular or almost triangular in equatorial outline, about 8–10.5 μm in diameter, and with monocolpate (Fig. 30) or trichotomocolpate apertures (Fig. 31). The two aperture types co-occur in the same stamen and were clearly produced by the same plant. The tectum has a finely striate supratectal ornamentation that forms a fingerprint-like pattern (Figs. 31–33).

The pollen grains have been observed in situ in several flowers from the Vale de Agua and Famalicão floras. The same flower type also occurs in the floras from Buarcos and Catefica, but no pollen was observed in these specimens.

A.2. Dicolpate pollen (Figs. 34–38). Pollen grains very similar to the monocolpate-trichotomocolpate grains described above, but distinct in having a dicolpate aperture configuration (Figs. 34, 37), and in being larger with an equatorial diameter of about 13.5–15 μm. Pollen grains of this species also differ in having slightly finer striations on the tectum (Figs. 35, 36, 38). The two colpi are parallel and closely spaced and extend almost to the equator of the grains. The margins of the colpi are distinctly marked by a smooth tectum. The striate ornamentation becomes less prominent toward the aperture margins, and in the narrow intercolpal area the pollen wall is psilate (Figs. 34, 37). A fracture in the pollen wall shows that the pollen grains have apparently a granular infratectal structure (Fig. 38).

The pollen grains were observed in situ in several flowers from the Vale de Agua flora. Similar flowers are also known from the Buarcos flora, but no pollen grains were observed in the Buarcos specimens.

B. Monoaperturate, tectate, psilate pollen with foveolate or reticulate equatorial zone (Figs. 39–49). Four different pollen types have been grouped together under this heading because they share the unusual feature of having psilate grains with a distinctive foveolate to reticulate equatorial zone. Such features are not common in angiosperm pollen. One of the pollen types is from the Vale de Agua flora, two are from the Buarcos, and one is from Torres Vedras. The Vale de Agua pollen type (Figs. 39, 40) apparently has a broader equatorial zone than the other three. In the two different types from the Buarcos flora (Figs. 41–46) the equatorial zone is foveolate, while in the polar regions the tectum is more or less psilate. The size and density of the foveolae differ in the two pollen types. In the pollen type from Torres Vedras (Figs. 47–49) the equatorial belt grades from foveolate to coarsely reticulate. All pollen types have similar granular membranes in the colpi. These types of pollen grains show some resemblance to pollen grains of the *Anacostia-Similipollis* type (pollen type F.1 and F.2, Figs. 83–85), which have a graded reticulate to foveolate reticulum that has smaller lumina and foveolae in the polar areas, and larger lumina in the equatorial region. This kind of graded tectum structure, here referred to as *Similipollis*-type grading (see pollen F), has been reported from extant palms (e.g., Harley, 1997) but is apparently not present in the pollen of extant magnoliid angiosperms. Another type of graded reticulum, here referred to as *Liliacidites*-type grading (see pollen type E), has smaller lumina in equatorial position at the ends of the apertures and is known for many monocotyledons (e.g., Erdtman, 1952; Alvarez & Köhler, 1987; Le Thomas et al., 1996).

B.1. Monocolpate, psilate-foveolate pollen (Figs. 39, 40). Pollen grains small, elliptical to circular in equatorial outline, and about 8.5–9 μm in diameter. Aperture monocolpate with rather short colpi and a granular colpus membrane (Fig. 39). Pollen wall psilate except for a broad foveolate zone around the equator (Fig. 40).

The pollen grains were observed in a small fragmentary stamen, about 0.4 mm long, from the Vale de Agua flora. We have not seen any reports of dispersed pollen taxa that match this pollen type.

B.2. Monocolpate, psilate-finely foveolate pollen (Figs. 41–43). Pollen grains elliptical in outline, and about 12–13.5 μm long. Aperture monocolpate with the colpus reaching almost to the equator of the grain (Fig. 41). Colpus membrane granular, and the colpus margin distinct. Pollen wall psilate with

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type B.3, monocolpate, finely foveolate pollen, S101739 (Buarcos sample 209). —44. Distal view showing monocolpate aperture and granular aperture membrane, ×4000; scale shown in Figure 39. —45. Oblique distal view showing trichotomocolpate aperture, ×4000; scale shown in Figure 39. —46. Proximal view showing foveolate equatorial zone, ×4000; scale shown in Figure 39. 47–49. Pollen type B.4, monocolpate, psilate-reticulate pollen, S105002 (Torres Vedras sample 144). —47. Distal view showing monocolpate aperture and granular aperture membrane, ×4000; scale shown in Figure 39. —48. Proximal view showing foveolate to reticulate equatorial zone, ×4000; scale shown in Figure 39. —49. Oblique lateral view showing colpus and equatorial zone, ×4000; scale shown in Figure 39.

scattered foveolae and with a narrow, finely foveolate zone around the equator (Figs. 42, 43).

The pollen grains were observed in situ in a stamen with tetrasporangiate anther from the Buarcos flora. We are not aware of any dispersed pollen taxon similar to this in situ form.

B.3. Monocolpate-trichotomocolpate, finely foveolate pollen (Figs. 44–46). Pollen grains almost circular in equatorial outline and about 9–11 μm in diameter. Aperture monocolpate or trichotomocolpate. Both aperture forms have been observed in situ in the same anther. Colpus reaches almost to the equator. Colpus margin is distinct and the colpus membrane granular. Pollen wall psilate grading into a narrow, foveolate equatorial zone.

The pollen grains were found in a small, fragmentary flower from the Buarcos flora consisting of two stamens and perianth parts. The stamens have distinct filaments and the anthers are tetrasporangiate. We are not aware that similar pollen grains have been illustrated from dispersed palynofloras.

B.4. Monocolpate, psilate-reticulate pollen (Figs. 47–49). Pollen grains almost circular in equatorial outline and about 9–12 μm in diameter. Aperture monocolpate with a long broad colpus reaching almost to the equator of the grain (Fig. 47). Colpus margin is distinct and the colpus membrane is granular. Tectum distinctly heterogeneous, psilate over most of the proximal and distal surfaces, with a narrow foveolate to reticulate zone around the equator and a narrow foveolate zone flanking the aperture margins (Figs. 48, 49).

This pollen type has been recovered in a tetrasporangiate anther from the Torres Vedras locality. The grains show some resemblance to dispersed pollen from the late Barremian-early Aptian of Gabon assigned to *Similipollis* Góczán & Juhász (Doyle & Hotton, 1991) that also has a narrow foveolate-reticulate equatorial zone, but the African pollen is distinct in having a long extended colpus.

C. Monoaperturate, tectate pollen with finely spiny ornamentation. Pollen grains monocolpate, elliptical (?) in equatorial outline, about 15 μm in diameter. Colpus margin and colpus membrane not well exposed. Grains are tectate. Tectum faintly rugulate-verrucate and covered by minute echinae.

The pollen is poorly preserved and not illustrated here. It occurs on a small spiny fruit very similar to those of *Appomattoxia ancistrophora* Friis, Pedersen & Crane described from the early to middle Albian Puddledock flora, Virginia, U.S.A. (Friis et al., 1995). The pollen is also closely similar to that of *Appomattoxia,* and comparable to dispersed grains from Lower Cretaceous strata assigned to *Tucanopollis* (Regali) Regali and *Transitoripollis* Góczán & Juhász (see discussion in Friis et al., 1995). In extant plants pollen of this type is known in the Piperales, and the fruits of *Appomattoxia* also show a possible relationship with extant members of the Piperales, although the fossils cannot with certainty be placed in this group.

D. Monoaperturate, semitectate, reticulate pollen with smooth muri (Figs. 50–74). Monoaperturate columellate pollen with a non-graded reticulum that lacks supratectal ornamentation on the muri is common among the in situ pollen types from the Portuguese floras. Pollen grains of this type have been found associated with diverse gynoecia and also in anthers. They vary in size, details of the reticulum, and length and spacing of the columellae. They probably represent several distinct genera, and probably also belong to different families, orders, or other higher-level taxa. Dispersed pollen grains similar to these Portuguese reticulate pollen have been described from several Early Cretaceous palynofloras and are often assigned to various species of the genus *Retimonocolpites* Pierce (e.g., Doyle & Robbins, 1977; Schrank, 1983; Ward, 1986). Several taxa of this general type were also

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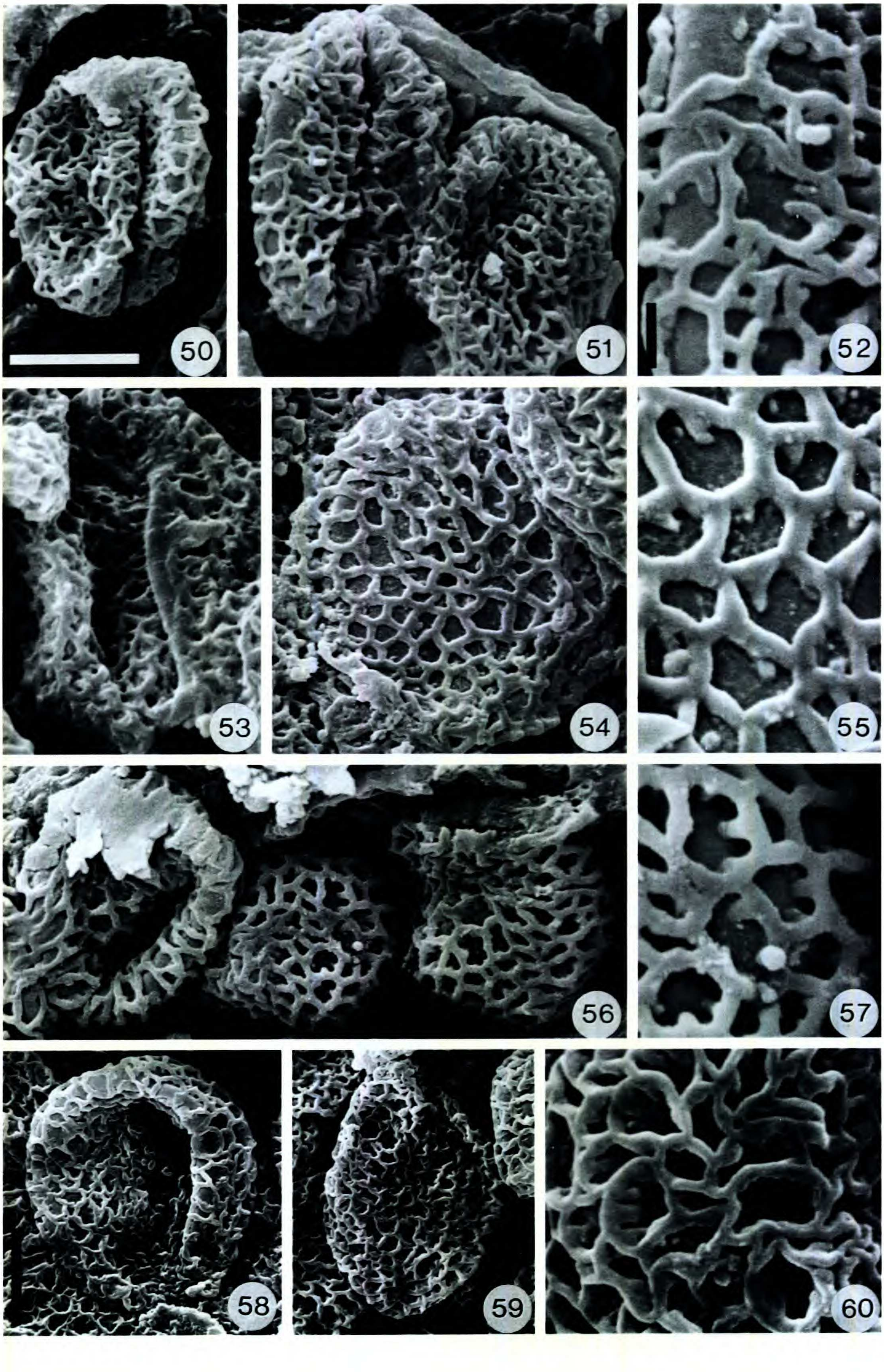
Figures 50–60. Scanning electron micrographs of pollen types D.1–D.4 from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 50–52. Pollen type D.1, monocolpate, heterogeneous reticulate pollen with widely spaced columellae, S105277 (Vale de Agua sample 19). —50. Distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —51. Two grains showing distal and proximal views, ×4000; scale shown in Figure 50. —52. Detail of reticulum showing widely spaced columellae, ×10,000; scale equal to 1 μm. 53–55. Pollen type D.2, monocolpate, homogeneous reticulate pollen with widely spaced columellae, S105256 (Vale de Agua sample 141). —53. Distal view showing monocolpate aperture, ×4000; scale shown in Figure 50. —54. Proximal view, ×4000; scale shown in Figure 50. —55. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 52. 56, 57. Pollen type D.3, monocolpate, heterogeneous reticulate pollen with widely spaced columellae, S105029 (Vale de Agua sample 19). —56. Three grains showing distal and proximal views, ×4000; scale shown in Figure 50. —57. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 52. 58–60. Pollen type D.4, monocolpate, homogeneous reticulate pollen with densely spaced columellae, S105661 (Vale de Agua sample 139). —58. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —59. Proximal view, ×3000; scale shown in Figure 58. —60. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 52.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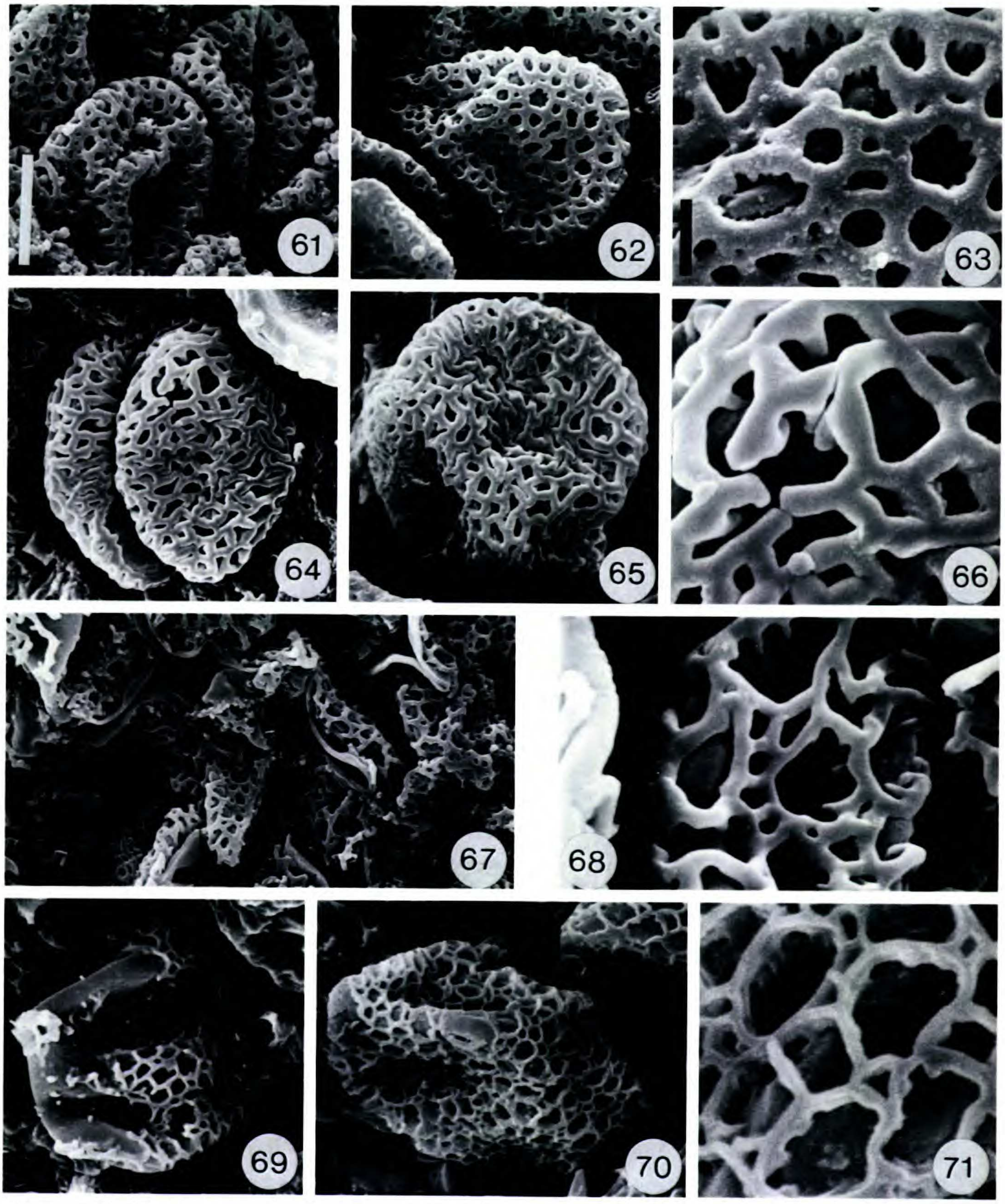
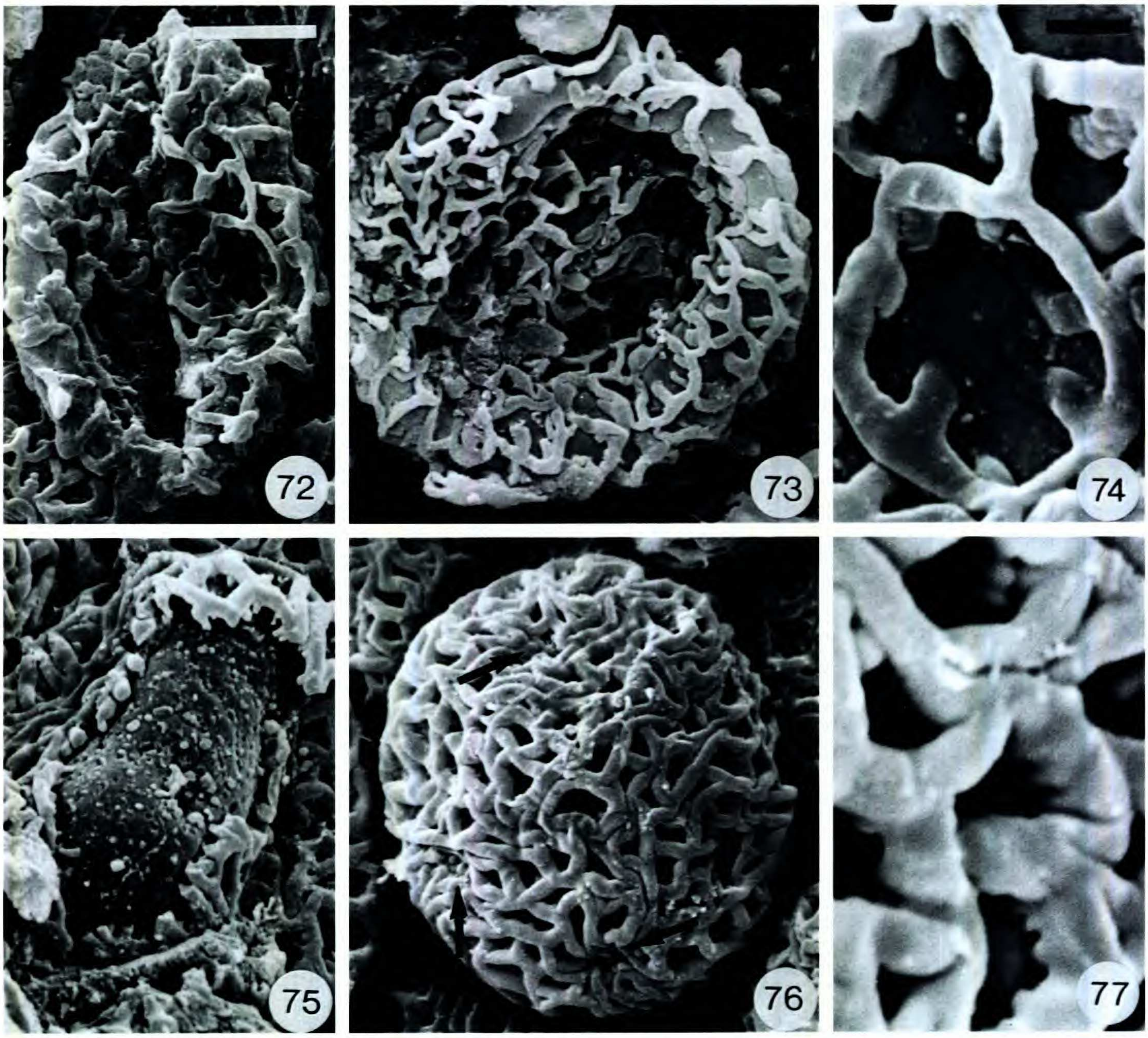


Figures 61–71. Scanning electron micrographs of pollen types D.5–D.8 from the Early Cretaceous (Barremian or Aptian?) Torres Vedras and Catefica floras, western Portugal. 61–63. Pollen type D.5, monocolpate, heterogeneous, reticulate pollen with densely spaced columellae, S101306 (Torres Vedras sample 39). —61. Two pollen grains in distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —62. Proximal view, ×3000; scale shown in Figure 61. —63. Detail of reticulum showing densely spaced columellae, ×10,000; scale equal to 1 μm. 64–66. Pollen type D.6, monocolpate, heterogeneous, reticulate pollen with widely spaced columellae, S105018 (Torres Vedras sample 44). —64. Oblique distal view showing monocolpate aperture, ×3000; scale shown in Figure 61. —65. Proximal view, ×3000; scale shown in Figure 61. —66. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 63. 67, 68. Pollen type D.7, monocolpate, heterogeneous reticulate pollen with densely spaced columellae, S105021 (Torres Vedras sample 44). —67. Numerous pollen grains showing distal and proximal views, ×3000; scale shown in Figure 61. —68. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 63. 69–71. Pollen type D.8, monocolpate, heterogeneous reticulate pollen with densely spaced columellae, S105281 (Catefica sample 151). —69. Proximal view of pollen grain with reticulum partially abraded, ×3000; scale shown in Figure 61. —70. Proximal view, ×3000; scale shown in Figure 61. —71. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 63.



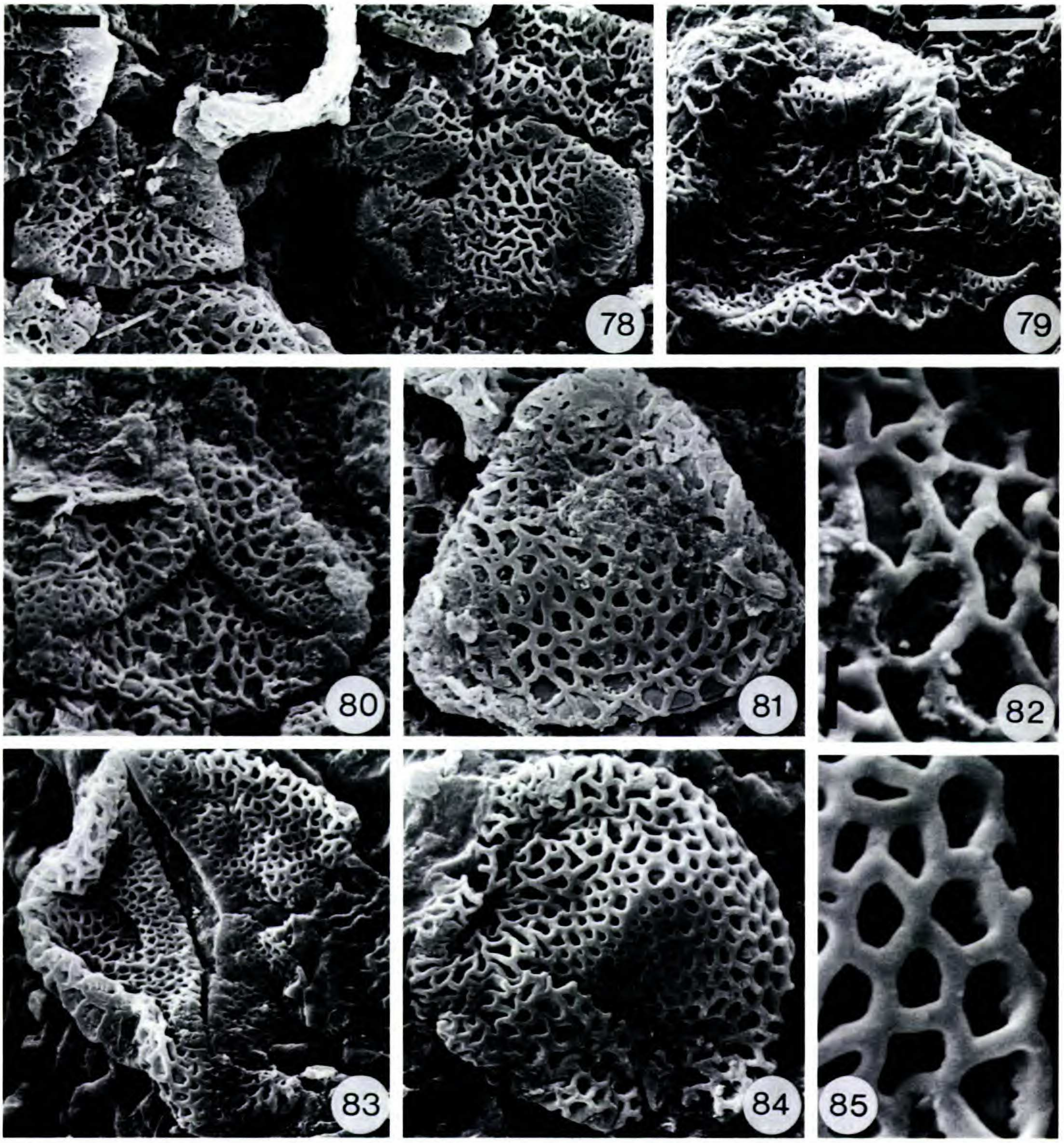
Figures 72–77. Scanning electron micrographs of pollen types D.9 and H from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 72–74. Pollen type D.9, monocolpate, homogeneous reticulate pollen with widely spaced columellae, S105285. —72. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —73. Proximal view, ×3000; scale shown in Figure 72. —74. Detail of reticulum showing widely spaced columellae, ×10,000; scale equal to 1 μm. 75–77. Pollen type H, periporate and reticulate pollen, S105073. —75. Pollen grain with reticulum partially abraded, ×3000; scale shown in Figure 72. —76. Pollen grain showing reticulum and location of several pores (arrows), ×3000; scale shown in Figure 72. —77. Detail of reticulum showing muri and columellae/granules, ×10,000; scale shown in Figure 74.

reported from Egypt by Penny (1991), who described forms with a heterogeneous reticulum (lumen size distribution bimodal) as various Biorecords of the Genusbox "Crocheret." Forms with a homogeneous reticulum (lumen size distribution unimodal) were described as Biorecords of the Genusbox "Reticoll." Most dispersed species of this general type are illustrated by LM images only and typically do not show the fine details of the reticulum and columellae that distinguish the pollen types from Portugal.

D.1. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 50–52). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 10.5–13 μm in diameter, and with a long colpus reaching to the equator (Figs. 50, 51). Reticulum is heterogeneous with lumina of various sizes. The smaller lumina are about 0.2–0.5 μm in diameter, and the larger are up to about 2 μm in diameter. Muri are narrow, smooth, and low, with rounded profile, about 0.3 μm wide. Columellae are long and widely spaced (Fig. 52).

These pollen grains were observed on the surface of small spiny fruits from the Vale de Agua flora.

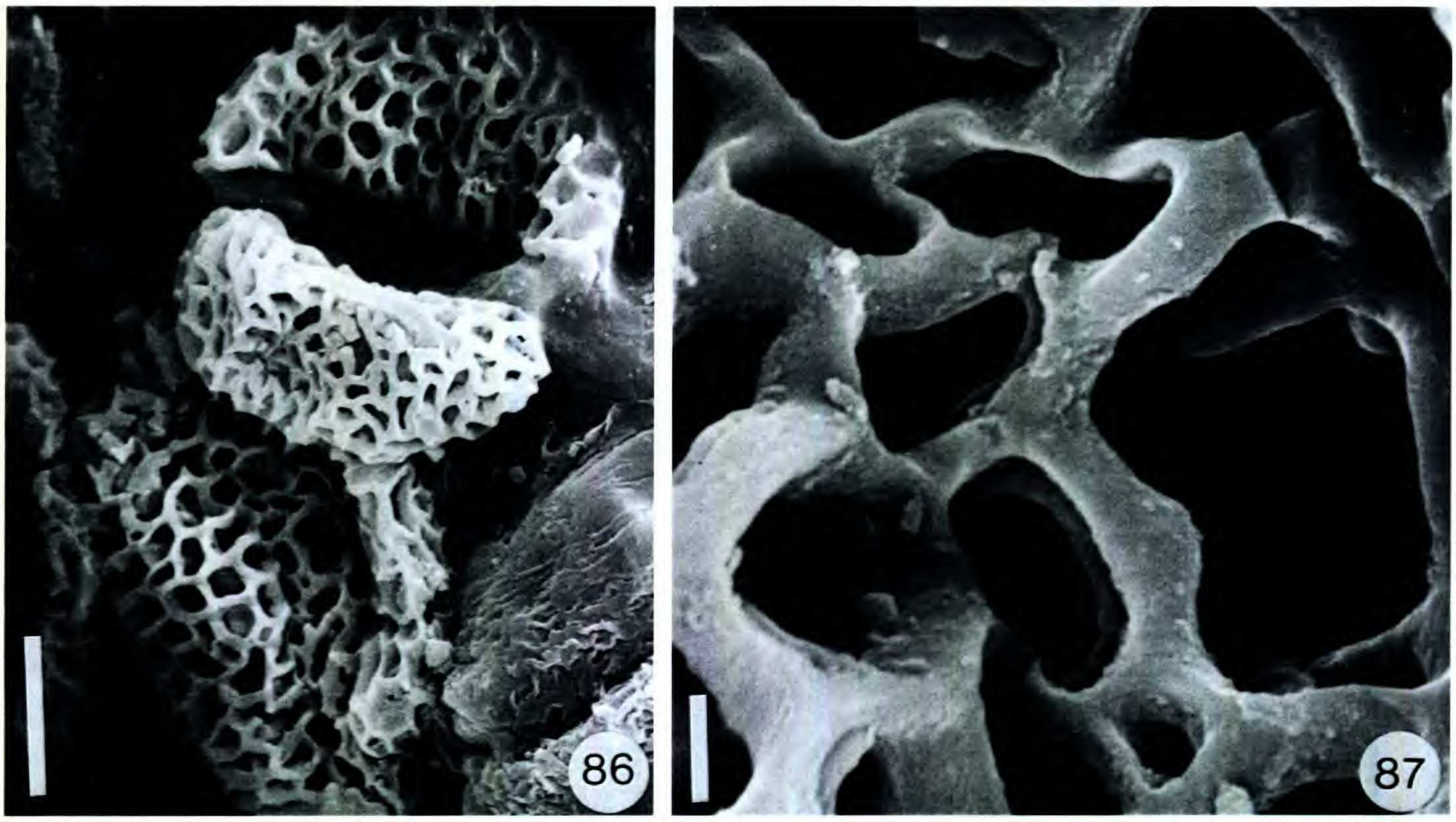
D.2. Monocolpate, homogeneous reticulate pollen with widely spaced columellae (Figs. 53–55). Pollen



Figures 78–85. Scanning electron micrographs of pollen type E and F from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. 78–82. Pollen type E, trichotomocolpate, semitectate, and reticulate pollen with graded reticulum and smooth muri, S101425. —78. Pollen grains showing distal and proximal views, ×2000; scale equal to 5 μm. —79. Distal view showing trichotomocolpate aperture, ×3000; scale equal to 5 μm. —80. Distal view showing trichotomocolpate aperture, ×3000; scale shown in Figure 79. —81. Proximal view, ×3000; scale shown in Figure 79. —82. Detail of reticulum showing short densely spaced columellae, ×10,000; scale equal to 1 μm. 83–85. Pollen type F.1, monocolpate-trichotomocolpate, and reticulate pollen with graded reticulum and smooth muri (*Anacostia portugallica*), S105039. —83. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 79. —84. Proximal view showing graded reticulum, ×3000; scale shown in Figure 79. —85. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 82.

grains monocolpate, circular in equatorial outline, about 14.5 μm in diameter, and with a long colpus reaching almost to the equator (Figs. 53, 54). Reticulum is homogeneous with lumina of about the same size all over the grain, up to about 1.5 μm in diameter (Fig. 55). Muri are low, with a rounded profile, and about 0.5 μm wide. Columellae are long and widely spaced.

These pollen grains were observed in stamen fragments with elongated pollen sacs, about 0.6 mm long, from the Vale de Agua flora. They are similar in shape and reticulum pattern to dispersed grains



Figures 86, 87. Scanning electron micrographs of pollen type G from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. Monocolpate reticulate pollen with extended colpus, S101303. —86. Distal view showing extended colpus, ×1500; scale equal to 10 μm. —87. Detail of reticulum showing long, widely spaced columellae, ×10,000; scale equal to 1 μm.

illustrated and described from the Potomac Group sequence (Zone IIB, middle to late Albian) as "*Liliacidites*" *minutus* (= *Clavatipollenites minutus* Brenner) (Walker & Walker, 1984), but the columellae are longer and more widely spaced. As pointed out by Walker and Walker (1984) this kind of pollen differs from typical *Liliacidites* Couper grains, which have a graded reticulum. According to Walker and Walker (1984) the "*Liliacidites*" *minutus* grains that they described are probably identical to grains occurring throughout the Potomac Group sequence and originally assigned by Brenner (1963) to *Clavatipollenites minutus* Brenner.

D.3. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 56, 57). Pollen grains monocolpate, more or less spherical in outline, and about 10–11 μm in diameter (Fig. 56). Colpus is weakly marked. Reticulum is heterogeneous with most lumina of more or less the same size, up to about 1.5 μm in diameter, but with some small lumina scattered over the surface. Muri are smooth and low, with a rounded profile, and about 0.4 μm wide. Columellae are medium-sized to short and widely spaced (Fig. 57).

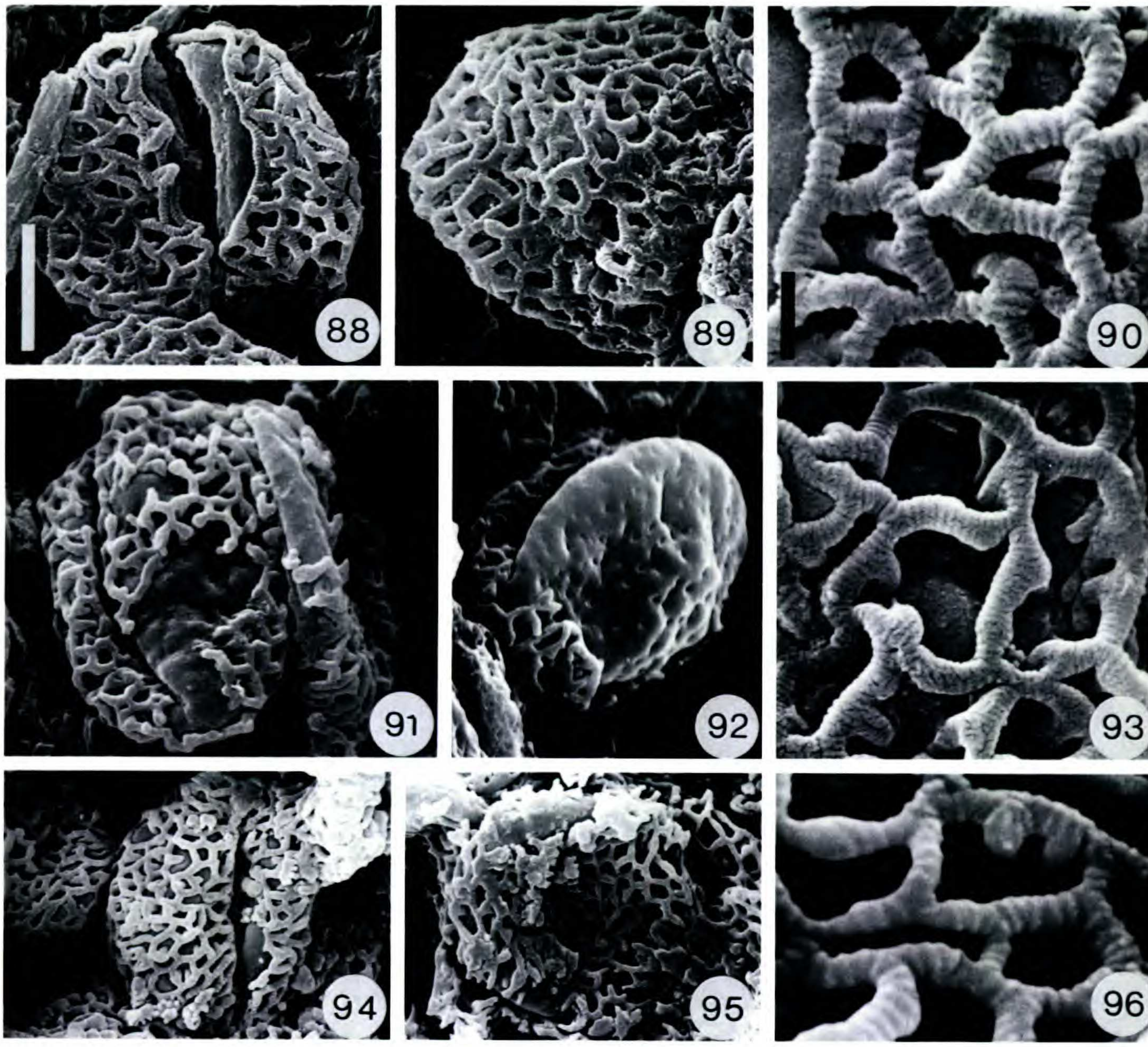
The pollen grains were found in situ in a dispersed tetrasporangiate anther, about 0.5 mm long, with few morphological details preserved, from the Vale de Agua flora.

D.4. Monocolpate, homogeneous reticulate pollen with densely spaced columellae (Figs. 58–60). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 13–14 μm in diameter (Figs. 58, 59). Colpus is broad and long, reaching almost to the equator. The colpus margin is indistinct, and the colpus membrane is verrucate. Reticulum is homogeneous with lumina of more or less equal size, up to about 1.2 μm in diameter. Muri are high and narrow, about 0.2 μm wide, with rounded to triangular profile. Columellae are short and densely spaced (Fig. 60).

The pollen was observed in a fragmentary stamen from the Vale de Agua flora.

D.5. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 61–63). Pollen grains monocolpate and elliptical to circular in outline, and about 12–13 μm in diameter (Figs. 61, 62). Colpus is long, reaching to the equator, and has a distinct margin. Reticulum heterogeneous and fine with larger lumina up to about 1.2 μm in diameter, and smaller lumina about 0.2 μm in diameter. Muri are low, with a rounded profile, and about 0.3 μm wide. Reticulum grades into a narrow foveolate to psilate zone along the colpus margin. Columellae are short and densely spaced (Fig. 63).

These pollen grains were found in situ in a small incompletely preserved and strongly abraded hypogynous and trimerous flower from the Torres Vedras flora.

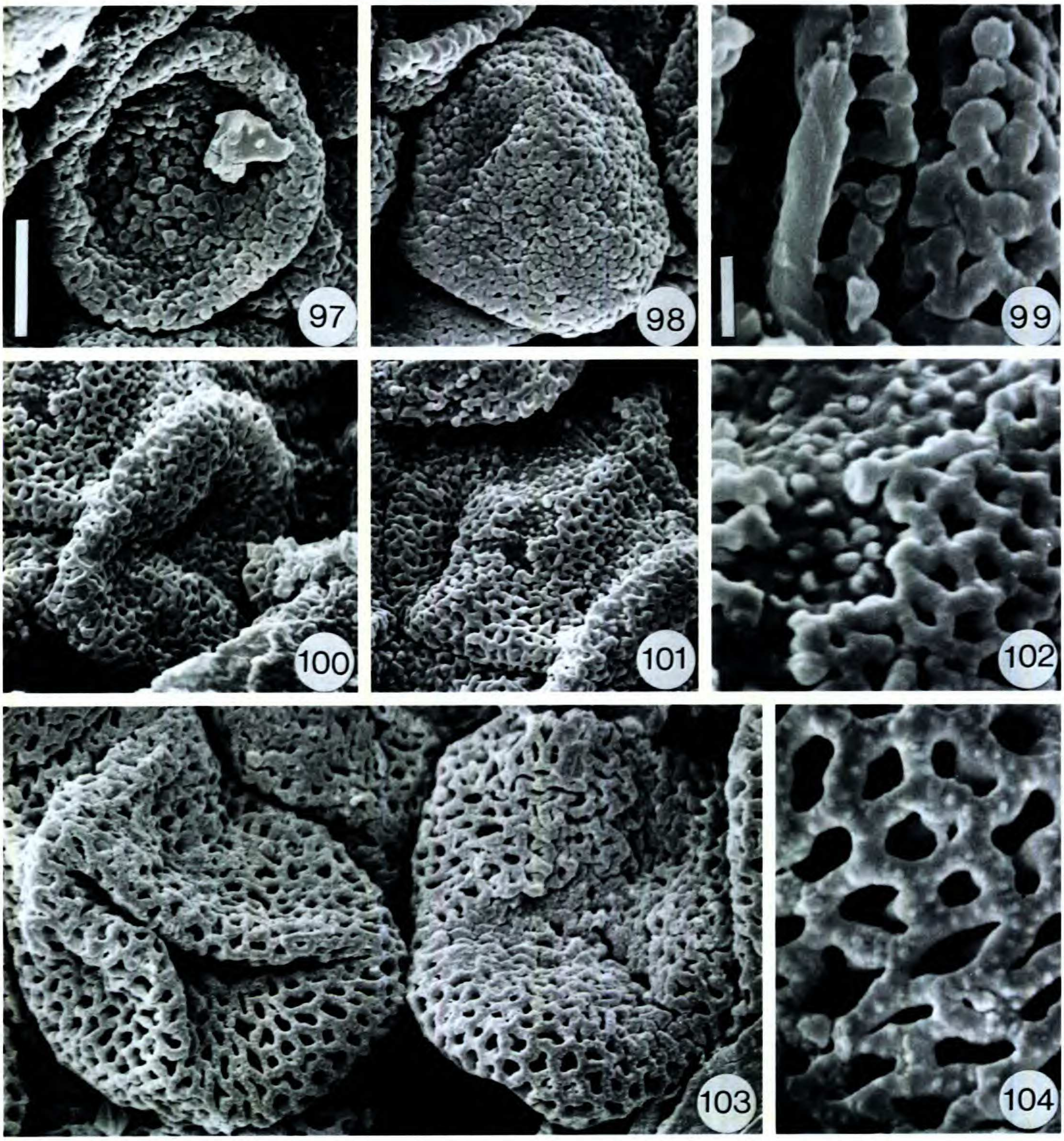


Figures 88–96. Scanning electron micrographs of pollen type I from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 88–90. Pollen type I.1, monocolpate, reticulate pollen with coarsely striate muri, S101316 (Vale de Agua sample 141). —88. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —89. Proximal view, ×3000; scale shown in Figure 88. —90. Detail of reticulum showing muri with coarse, transverse, striations and long columellae, ×10,000; scale equal to 1 μm. 91–93. Pollen type I.2, monocolpate, reticulate pollen with finely striate muri, S101320 (Vale de Agua sample 141). —91. Oblique distal view showing monocolpate aperture, note reticulum partially abraded and exposing the foot-layer, ×3000; scale shown in Figure 88. —92. Oblique lateral view showing partially abraded reticulum, ×3000; scale shown in Figure 88. —93. Detail of reticulum showing muri with fine, transverse, striations and long columellae, ×10,000; scale shown in Figure 90. 94–96. Pollen type I.3, monocolpate, reticulate pollen with weakly striate muri, S105602 (Vale de Agua sample 139). —94. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 88. —95. Proximal view, ×3000; scale shown in Figure 88. —96. Detail of reticulum showing muri with weak, transverse, striations, ×10,000; scale shown in Figure 90.

D.6. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 64–66). Pollen grains monocolpate, circular in equatorial outline, and about 11.5–13.5 μm in diameter. Colpus is long with a distinct margin, and appears to extend slightly beyond the equator (Figs. 64, 65). Reticulum is heterogeneous and loosely attached, with larger lumina up to about 1.2 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.5 μm wide. Columellae are medium in size to short and widely spaced (Fig. 66).

The pollen grains were found in a fragmentary stamen from the Torres Vedras flora.

D.7. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 67, 68). Pollen grains circular in equatorial outline and about 10 μm in diameter. Reticulum is heterogeneous and loosely attached. The smaller lumina are about 0.2–0.3 μm



Figures 97–104. Scanning electron micrographs of pollen types J.1–J.3 from the Early Cretaceous (Barremian or Aptian?) Torres Vedras flora (sample 44), western Portugal. 97–99. Pollen type J.1, monocolpate pollen with a round aperture, dense reticulum and broad muri, S105019. —97. Distal view showing round aperture, ×3000; scale equal to 5 μm. —98. Proximal view, ×3000; scale shown in Figure 97. —99. Detail of reticulum and exine structure, ×10,000; scale equal to 1 μm. 100–102. Pollen type J.2, trichotomocolpate pollen with dense reticulum and broad muri, S105015. —100. Oblique distal view showing trichotomocolpate aperture, ×3000; scale shown in Figure 97. —101. Proximal view, ×3000; scale shown in Figure 97. —102. Detail of reticulum; note foot layer and columellae exposed where reticulum is partially abraded, ×10,000; scale shown in Figure 99. 103–104. Pollen type J.3, trichotomocolpate pollen with dense reticulum and broad muri, S105012. —103. Distal view of two pollen grains showing trichotomocolpate aperture, ×3000; scale shown in Figure 97. —104. Detail of reticulum with blunt protrusions, ×10,000; scale shown in Figure 99.

in diameter, and are often arranged in rows around the larger lumina, which are up to about 1.7 μm in diameter. Muri are narrow and low, with a rounded profile, and about 0.2 μm wide. Columellae are medium in size and densely spaced (Fig. 68).

The pollen grains were found in a fragmentary stamen from the Torres Vedras flora. Dispersed pollen grains from Egypt assigned by Penny (1991) to "Crochetret-Tallmur" have a comparable heterogeneous reticulum with smaller lumina in rows. How-

ever, the Egyptian grains are much larger than those from Portugal.

D.8. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 69–71). Pollen grains monocolpate, circular in equatorial outline, about 15.5 μm in diameter. Reticulum is heterogeneous and loosely attached. Larger lumina are up to about 1.6 μm in diameter. Smaller lumina are 0.2–0.3 μm in diameter, sometimes arranged in rows. Muri narrow with an almost triangular profile, about 0.2 μm wide. Columellae very short and densely spaced (Fig. 71).

The pollen grains were found in a fragmentary laminar, dithecate and tetrasporangiate stamen from the Catefica flora. The pollen sacs are arranged in two pairs on the same side of the stamen. There is abundant sterile tissue between the two pairs of pollen sacs and also lateral to them. The stamen is broken both distally and proximally. The pollen grains resemble those described above from the Torres Vedras flora (pollen type D.7), but the columellae are shorter and more densely spaced.

D.9. Monocolpate, homogeneous reticulate pollen with widely spaced columellae (Figs. 72–74). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 16.5–20.5 μm in diameter (Figs. 72, 73). All grains observed appear to be infolded over the aperture, and neither aperture margin nor aperture membrane has been observed. Reticulum is coarse and loosely attached. Lumina are of more or less equal size over the whole grain, up to about 4.5 μm in diameter. Muri are narrow and high with a rounded to triangular profile, sometimes with a narrow crest, and about 0.4 μm wide. Columellae are long and widely spaced (Fig. 74).

This pollen type occurs abundantly on the surface of small fruits with resin bodies from the Famalicão flora (Figs. 1–6). The fruits contain two endotestal and anatropous seeds with a layer of distinct crystal cells. Anatomically and morphologically the seeds are similar to those of some extant Magnoliaceae, but fruit and pollen features are unlike those of this family. The same kind of fruit has been seen in the fossil floras from Vale de Agua, Catefica, and Buarcos, but pollen grains have not been observed on the fruits from any of these other floras.

D.10. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae. Pollen grains elliptical in equatorial outline, and about 10–11 μm in diameter. Aperture monocolpate with short colpus, and distinct aperture margin. Reticulum is heterogeneous with smaller lumina along the aperture margin. Muri are broad and smooth, with a rounded profile, about 0.2 μm wide. Columellae are of medium size and widely spaced.

The pollen is poorly preserved and not illustrated here. It occurs in a small fragmentary anther from the Famalicão flora.

D. 11. Monocolpate, homogeneous reticulate pollen. Pollen grain elliptical to circular in equatorial outline and about 13 μm in diameter. All grains are strongly folded, and aperture configuration is difficult to study. Reticulum dense with broad, low muri. Columellae not visible in any of the grains.

The pollen is poorly preserved and not figured here. It occurs on the stigmatic surface of a small rugulate fruit with sessile stigma from the Catefica flora.

D.12. Monocolpate, homogeneous reticulate pollen with widely spaced columellae. Pollen grains elliptical in equatorial outline, about 12 μm in diameter. Aperture monocolpate with long colpus extending to the equator. Reticulum homogeneous, loosely attached. Lumina are about 0.7 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.35 μm wide. Columellae are long and widely spaced.

The pollen occurs in a small tetrasporangiate anther from the Catefica flora. They are not figured here.

D. 13. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae. Pollen more or less spherical in outline, about 10–11 μm in diameter. Aperture monocolpate with long colpus reaching to the equator. Aperture margin is distinct. Reticulum is homogeneous, loosely attached. Larger lumina are up to about 1.4 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.35 μm wide. Columellae are long and widely spaced.

The pollen grains were found in a small group of stamens from the Torres Vedras locality. They are not figured here.

E. Trichotomocolpate and semitectate, reticulate pollen with Liliacidites-type grading of reticulum (Figs. 78–82). One pollen type with a reticulum that grades into smaller lumina or almost psilate areas toward the ends of the aperture arms (in the equatorial region) has been observed in the Early Cretaceous floras of Portugal. This kind of graded reticulum is characteristic for many extant members of Liliales, Asperagales, and other monocotyledons (e.g., Erdtman, 1952; Alvarez & Köhler, 1987; Le Thomas et al., 1996). Dispersed fossil pollen grains with this type of reticulum were first described as *Liliacidites* (Couper, 1953) from the Late Cretaceous of New Zealand and have been

reported from numerous Cretaceous palynofloras (Doyle et al., 1977; Doyle & Robbins, 1977; Walker & Walker, 1984; Ward et al., 1989). *Liliacidites*-type pollen from the Aptian of Egypt was assigned to the Biorecord "Crochetret-Endsmall" (Penny, 1991). We refer to this kind of grading of the reticulum as *Liliacidites*-type grading in contrast to the *Similipollis*-type of grading, in which the larger lumina occur around the equator and decrease in size toward the aperture margins and the proximal pole (see pollen type F).

The Portuguese pollen grains are triangular in equatorial outline and about 13.5–16 μm in diameter (Figs. 78–80). Aperture is trichotomocolpate. Arms of aperture long, extending over the equatorial rim to the proximal side of the grain (Figs. 78, 79). Only trichotomocolpate forms were observed in the anther, and apparently this plant produced only pollen grains with one type of aperture (in contrast to the *Anacostia*-plant described below, pollen type F.1 and F.2). Aperture margin is distinct. Tectum is coarsely reticulate over most of the grain with lumina up to about 1.5 μm in diameter. Toward the aperture margin and around the three corners of the grains at the ends of the aperture arms the reticulum grades into a narrow foveolate to psilate zone (Fig. 78). Muri are low, with rounded profile and a smooth surface, about 0.3 μm wide. They are supported by short, densely spaced columellae (Fig. 82). Ultrathin sections of the grains show that the pollen wall has a thick foot layer and well-developed endexine under the aperture.

The pollen grains were observed in a dispersed stamen from the Vale de Agua flora. The stamen is about 1 mm long and consists of a short, broad filament bearing a tetrasporangiate anther with a triangular apical extension of the connective (Friis et al., 1994b, fig. 8d).

These pollen grains are similar to dispersed grains assigned to *Liliacidites* in having the foveolate-psilate part of the tectum concentrated around the aperture margin and at the ends of the aperture arms, but *Liliacidites* typically has a monocolpate aperture. Monocolpate *Liliacidites* grains illustrated from the Potomac Group sequence (Zone IIB, middle-late Albian) have similar low, rounded and psilate muri supported by short, densely spaced columellae, but the foot layer is extremely thin in these grains. A graded reticulum, similar to that of *Liliacidites*, is known for pollen of several monocotyledonous plants (e.g., Liliaceae) and to our knowledge has not been reported from the Magnoliidae. Previous authors (e.g., Doyle, 1973; Walker & Walker, 1984) also noted several monocotyledonous features for the North American *Liliacidites* grains.

F. Monocolpate, semitectate, and reticulate pollen with Similipollis-type grading of reticulum (Figs. 83–85). Two-pollen type with a graded reticulum in which the lumina decrease in size from the equatorial area toward the aperture margins and proximal pole. Dispersed pollen grains with a comparable graded reticulum have been reported from various Early Cretaceous palynofloras in Europe, North America, and Africa (Doyle, 1973; Doyle et al., 1977; Walker & Walker, 1986). The genus *Similipollis* was established to accommodate this kind of dispersed fossil pollen (Góczán & Juhász, 1984), but in earlier studies such grains were typically assigned to the genera *Liliacidites* and *Retimonocolpites* (see discussion in Friis et al., 1997a). Pollen grains of this type closely resemble those of some extant palms (Walker & Walker, 1986; Harley, 1997). We refer to this kind of grading as the *Similipollis*-type to distinguish it from the type of grading in which the smaller lumina occur at the ends of the aperture in the equatorial regions (*Liliacidites*-type grading, see pollen type E).

F.1. Monocolpate-trichotomocolpate pollen (Anacostia portugallica) (Figs. 83–85). Pollen grains more or less circular in equatorial outline and 14.5–18.3 μm in diameter. Aperture is symmetrical or asymmetrical monocolpate or trichotomocolpate (Fig. 83). Arms of the aperture sharply delimited with rounded ends. Tectum is foveolate to reticulate with lumina decreasing in size toward the aperture and toward the proximal pole (Figs. 83, 84). Larger lumina are up to about 1.2 μm. Muri are smooth and low, with rounded profile, and about 0.35–0.4 μm wide. Columellae are short and densely spaced (Fig. 85).

This pollen type was found associated with the fruits of *Anacostia portugallica* in the Vale de Agua flora (Friis et al., 1997a). Fruits of *Anacostia portugallica* with pollen grains attached to the surface have also been recorded from the Buarcos flora. Fruits of this species also occur in the Famalicão flora, but none of these have pollen preserved. Fruits assigned to another species of *Anacostia*, *A. teixeirae*, occur abundantly in the Famalicão flora and are also reported from Buarcos, and pollen grains observed on a specimen from Famalicão are very similar to those of *A. portugallica*. In the Potomac Group sequence numerous fruits of *Anacostia* have been recovered from the Kenilworth and Puddledock localities. These are assigned to two distinct species: *A. marylandensis* Friis, Crane & Pedersen and *A. virginiensis* Friis, Crane & Ped-

ersen, both with similar monocolpate-trichotomocolpate grains adhering to the stigma and fruit wall (Friis et al., 1997a). The pollen grains in the two North American species and the Portuguese material are distinguished from each other by subtle details of the reticulum.

Although the pollen adhering to *Anacostia* show resemblance to that of some palms, the *Anacostia* fruiting units are unlike palm fruits and show some similarities in fruit and seed characters to magnoliid taxa (Friis et al., 1997a).

F.2. Monocolpate-trichotomocolpate pollen (Anacostia teixeirae). Pollen grains observed on the fruits of *Anacostia teixeirae* from the Famalicão flora are poorly preserved. They are closely similar to those of *A. portugallica* in form and reticulum grading but are slightly smaller, about 11–13 μm in diameter. Fruits of this species also occur in the Buarcos flora, but no pollen was observed on this material.

G. Monocolpate, semitectate, reticulate pollen with extended colpus (Figs. 86, 87). One monocolpate pollen type with a distinctly extended colpus has been observed in the Early Cretaceous floras from Portugal. Pollen grains are circular in equatorial outline and about 23–25 μm in diameter. Colpus is long, extending beyond the equator (Fig. 86), but its total extent is not clear in any of the specimens observed. Tectum is coarsely reticulate. Lumina typically of the same size, up to about 4.5 μm in diameter, with a few smaller lumina scattered over the grain. Muri are high with an acute triangular profile and about 0.6 μm wide. Columellae are long and widely spaced (Fig. 87).

The pollen grains were found in a dispersed stamen from the Vale de Agua flora figured by Friis et al. (1994b, fig. 8a, b). The stamen is dorsiventrally flattened and has a strongly thickened filament that is not well differentiated from the anther. The fertile portion of the stamen is small compared to the rest of the structure. The anther is dithecate and tetrasporangiate with two pairs of pollen sacs in a lateral position separated by a massive connective. The connective is extended apically into an almost quadrangular protrusion above the pollen sacs. The filament and connective have irregular hemispherical swellings on the surface that are thought to indicate the position of ethereal oil cells. We have not identified similar dispersed pollen in any Early Cretaceous palynoflora.

H. Periporate, semitectate, reticulate pollen (Figs. 75–77). One periporate pollen type has been observed in the Early Cretaceous floras of Portugal. Pollen grains almost spherical in outline, about 19 μm in diameter (Fig. 76). Pores are poorly defined and are seen as small, slightly sunken granular areas that are scattered over the entire grain (Figs. 75, 76). Pollen wall is coarsely reticulate with a homogeneous reticulum. The reticulum often appears contracted with muri closely appressed. Lumina are up to about 2 μm in diameter. Muri are smooth and high, with a rounded to triangular profile, about 0.5 μm wide. Columellae are short, densely spaced, and sometimes have the appearance of granulae rather than columellae (Fig. 77).

The pollen grains were found in a tetrasporangiate anther from the Famalicão locality. Dispersed pollen matching these in situ grains has not been observed in Cretaceous palynofloras as far as we are aware. The pollen grains are closely similar to those of the extant genus *Sarcandra* Gard. of the Chloranthaceae, but the stamen differs from those of modern *Sarcandra* and *Chloranthus* Sw. (the other insect-pollinated genus of the Chloranthaceae) in having larger pollen sacs and in lacking an extensive connective between them. Periporate pollen also occur in several monocotyledonous families (Dahlgren & Clifford, 1981). Eudicototyledonous taxa with periporate pollen occur in widely separate orders.

I. Monoaperturate, semitectate, reticulate pollen with transversely striate muri (Figs. 88–96). Three closely similar pollen types have been found in the Portuguese fossil floras. All three occur in the Vale de Agua flora, and one type also occurs in the Famalicão flora. They are distinguished from each other mainly by their size and details of the supratectal ornamentation, which varies from very fine in one species (Figs. 91–93) to relatively coarse in the two other species (Figs. 88–90, 94–96). Dispersed pollen comparable to these three types has been tentatively assigned to *Retimonocolpites* (Walker & Walker, 1984). From Egypt Penny (1991) assigned similar pollen with striate muri from the late Barremian-early Aptian to the biorecord "Reticoll-Springmur." Similar grains have also been reported from the Barremian of southern England as various forms of the biorecords "Barremian-teebac" (Hughes, 1994) and "Retisulc-muriverm" (Hughes & McDougall, 1987).

I.1. Monocolpate pollen with coarsely striate muri (Figs. 88–90). Pollen grains elliptical to spherical in outline, about 13–14 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Fig. 88). Colpus margin is distinct. Tectum is reticulate with a homogeneous reticulum and lumina of more or less equal size, up to about 2 μm in diameter. Muri are low, with a rounded pro-

file, about 0.4 μm wide. They are ornamented with distinct transverse ridges that give the muri a coarse transversely striate appearance. Columellae are long and widely spaced (Fig. 90).

The pollen grains occur in a small stamen with resin bodies from the Vale de Agua flora and have also been found in the same flora on the surface of small unilocular fruits and single-seeded hairy fruits. Very similar pollen also occurs abundantly on a fruit type from the Famalicão flora, but this fruit type differs from that of the Vale de Agua flora in several respects.

I.2. Monocolpate pollen with finely striate muri (Figs. 91–93). Pollen grains elliptical to spherical in outline, about 12–14 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Figs. 91–92). Colpus margin is distinct. Tectum is reticulate with a homogeneous, loosely attached reticulum and lumina of more or less equal size, up to about 2.5 μm in diameter. Muri are low, with a rounded profile, about 0.3 μm wide. They are ornamented with fine, densely spaced transverse ridges that give the muri a fine transversely striate appearance. Columellae are long and more closely spaced than in pollen type I.1 (Fig. 93).

The pollen grains were found on the surface of a hairy fruiting structure from the Vale de Agua flora, and were also observed in a fragmentary stamen from the Torres Vedras flora.

I.3. Monocolpate pollen with coarsely striate muri (Figs. 94–96). Pollen grains elliptical to spherical in outline, about 10–11 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Figs. 94, 95). Colpus margin is distinct. Tectum is reticulate with a homogeneous and loosely attached reticulum and lumina of more or less equal size, up to about 2 μm in diameter. Muri are low, with a rounded profile, about 0.3 μm wide. They are ornamented with transverse ridges that give the muri a coarse transversely striate appearance. Columellae are short and widely spaced (Fig. 96).

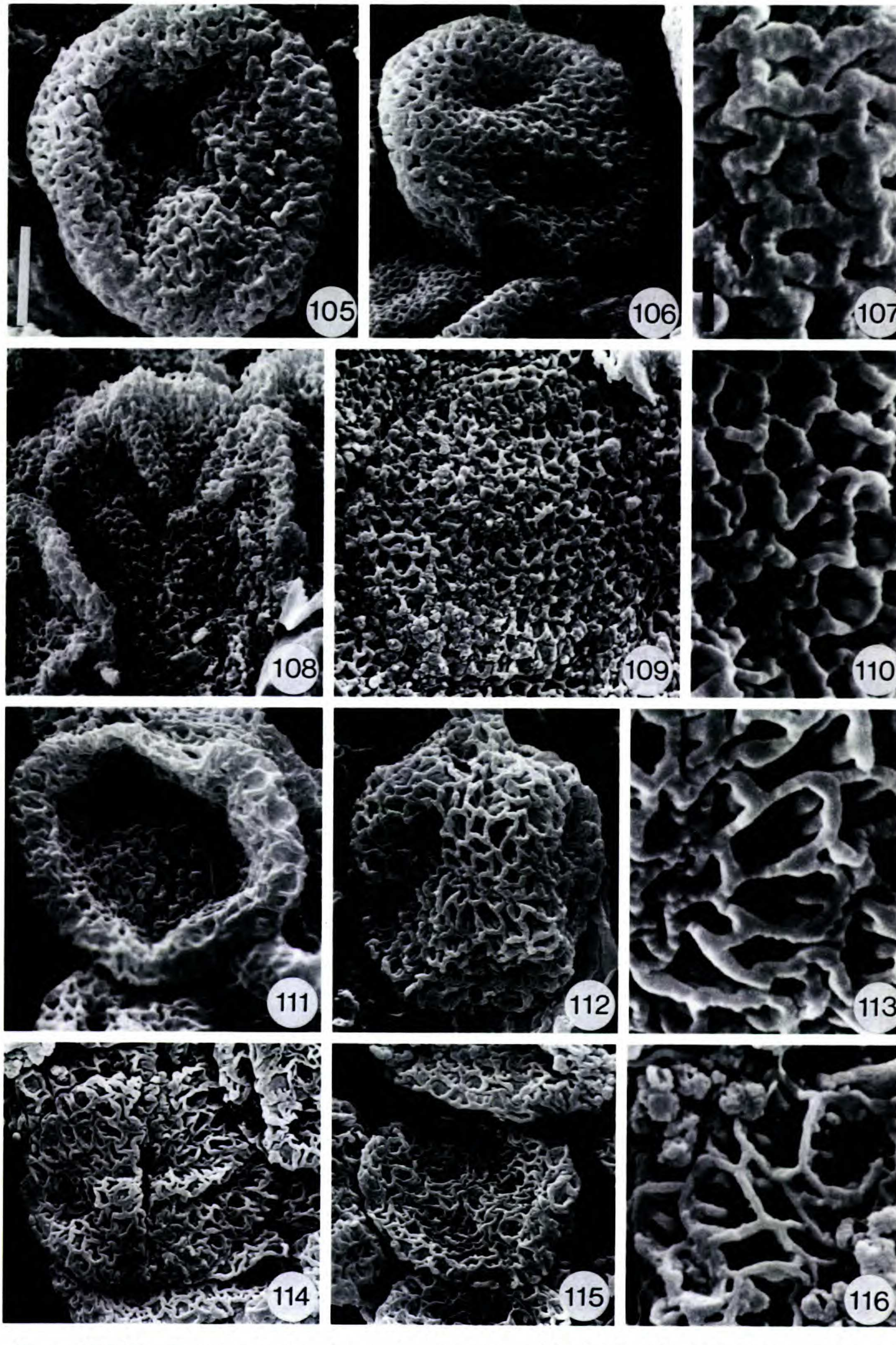
This pollen type is slightly smaller than the two other pollen types with striate muri (I.1, I.2). Ornamentation of the muri is rather coarse and similar to that described for pollen type I.1, but lumina are larger. The pollen grains were found in a well-preserved tetrasporangiate anther from the Vale de Agua flora.

J. Monocolpate, trichotomocolpate, and pentachotomocolpate, semitectate, reticulate pollen with beaded muri (Clavatipollenites-Asteropollis-type) (Figs. 97–121). Several closely similar pollen types with mono-, trichotomo-, and tetrachotomocolpate apertures and beaded ornamentation of the muri have been found in all five of the Portuguese floras. Pollen of this general type is also common in dispersed palynofloras from the Early Cretaceous, where they are typically assigned to species of *Clavatipollenites* and *Asteropollis* Hedlund & Norris. From the Early Cretaceous of southern England similar grains were assigned to the biorecord taxa "Retichot-baccat," "Retisulc-monbac," "Aptianlongcol," and "Retisulc-dident" (Hughes, 1994), and one type with beaded muri was reported from the late Barremian of Egypt as "Reticoll-speckle" (Penny, 1991). Species of *Clavatipollenites* have been compared to pollen of extant *Ascarina* (Couper, 1958; Walker & Walker, 1984), while species of *Asteropollis* have been compared to pollen of extant *Hedyosmum* (Walker & Walker, 1984); both are Chloranthaceae. The Chloranthaceae affinity of at least some *Asteropollis* pollen has now been established by the discovery of pollen grains associated with *Hedyosmum*-like pistillate flowers and stamens in the Early Cretaceous floras of Portugal (see above). However, monoaperturate pollen with beaded ornamentation of the muri also occur outside the Chloranthaceae (e.g., Lactoridaceae, Saururaceae; Walker, 1976), and some of the pollen types may belong to other families.

J.1. Monoaperturate pollen with a round aperture, dense reticulum, and broad muri (Figs. 97–99). Pollen grains almost circular in equatorial outline (Figs. 97, 98), about 14–16 μm in diameter, with a broad and round aperture that is indistinctly delimited and has a verrucate colpus membrane (Fig. 97). Tectum is densely reticulate. Lumina are typically condensed, about 0.6 μm in diameter. Muri are low, with a rounded profile, about 0.5 μm wide. They are ornamented with very small blunt protrusions that are often arranged in two rows along the edge of the muri. Columellae are of medium size and spacing (Fig. 99).

The pollen grains were found in stamens from the Torres Vedras locality.

J.2. Trichotomocolpate pollen with dense reticulum and broad muri (Figs. 100–102). Pollen grains circular in equatorial outline and about 12.5–13.5 μm in diameter (Figs. 100, 101). In most specimens the aperture is not visible, but in all grains where the aperture is visible it appears be trichotomocolpate with rather short arms. Tectum is semitectate and densely reticulate with lumina up to about 0.6 μm in diameter. Muri are low, with rounded profile, about 0.3 μm wide. They are ornamented with very small blunt protrusions that are



Figures 105–116. Scanning electron micrographs of pollen types J.4 —J.7 from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 105–107. Pollen type J.4, trichotomo- to tetrachotomocolpate pollen

often arranged in two rows. Columellae are of medium size and spacing.

The pollen grains were observed in a group of several stamens from the Torres Vedras flora (Fig. 3). The arrangement of the stamens shows that they were originally arranged in densely spaced whorls. The anthers are tetrasporangiate and elongated, about 0.7 mm long. The arrangement and shape of the stamens is similar to that seen in male inflorescences of extant *Hedyosmum* of the Chloranthaceae. This pollen type is very similar to that described above (pollen type J.1) in shape and reticulum pattern but differs in its clearly different aperture configuration.

J.3. Trichotomocolpate pollen with dense reticulum and broad muri (Figs. 103, 104). Pollen grains almost circular in equatorial outline and about 18–22 μm in diameter (Fig. 103). Aperture weakly defined, trichotomocolpate with aperture arms that reach almost to the equator, and a verrucate colpus membrane. Tectum is semitectate with a relatively dense homogeneous reticulum with lumina up to about 1.2 μm in diameter. Muri are low, with rounded profile, about 0.4 μm wide. They are ornamented by very small blunt protrusions that are typically arranged in two rows. Columellae are of medium size and widely spaced (Fig. 104). This pollen type shows resemblance to pollen type J.1 and J.2 in shape and tectum structure, but it is larger and has somewhat larger lumina.

The pollen grains were observed in an elongate tetrasporangiate anther, about 0.7 mm long, from the Torres Vedras flora.

J.4. Trichotomo- to pentachotomocolpate pollen with dense reticulum and broad muri (Figs. 105–107). Pollen grains more or less circular in outline, about 15–20 μm in diameter (Figs. 105, 106). Aperture trichotomo-, tetrachotomo-, or pentachotomocolpate with short aperture arms, weakly defined aperture margin, and verrucate aperture membrane. Tectum is densely reticulate with lumina of approximately equal size, up to about 1.5 μm in diameter. Muri are low, with rounded profile, about 0.5 μm wide. They are ornamented by very small blunt protrusions that are often arranged in two rows. Columellae are of medium size and spacing (Fig. 107).

Pollen grains of this type have been found in stamens and on the surface of *Hedyosmum*-like pistillate flowers from the Catefica, Torres Vedras, Vale de Agua, and Buarcos localities. *Hedyosmum*-like pistillate flowers also occur in the Famalicão flora, but no pollen was observed in this material.

J.5. Monoaperturate (monocolpate to tetrachotomocolpate?) pollen with open reticulum and narrow muri (Figs. 108–110). Pollen grains more or less circular in equatorial outline and about 16–17 μm in diameter (Figs. 108, 109). The aperture is very indistinct, apparently with up to four or five arms and verrucate colpus membrane. Tectum with an open reticulum and lumina of more or less equal size up to about 1.5 μm in diameter. Muri are narrow and low, with a rounded profile, and about 0.2 μm wide. They are ornamented by low blunt protrusions arranged in a single row. Columellae are long, broad, and medium spaced (Fig. 110).

This type of pollen was recovered in an elongated stamen, about 0.7 mm long, from the Vale de Agua flora.

J.6. Monoaperturate pollen with an irregular aperture, open reticulum and narrow muri (Figs. 111–113). Pollen grains more or less circular in equatorial outline and about 15 μm in diameter (Figs. 111, 112). The aperture is broad and weakly delimited, irregularly rounded to slightly triangular in outline. The tectum is open reticulate with lumina of more or less the same size, up to about 2.5 μm in diameter. Muri are narrow and low, with a rounded profile, about 0.3 μm wide. They are ornamented by small blunt protrusions arranged in a single row. Columellae are high and occasionally densely spaced (Fig. 113).

The pollen occurs in a fragmentary stamen, about 0.6 mm long, from the Vale de Agua flora,

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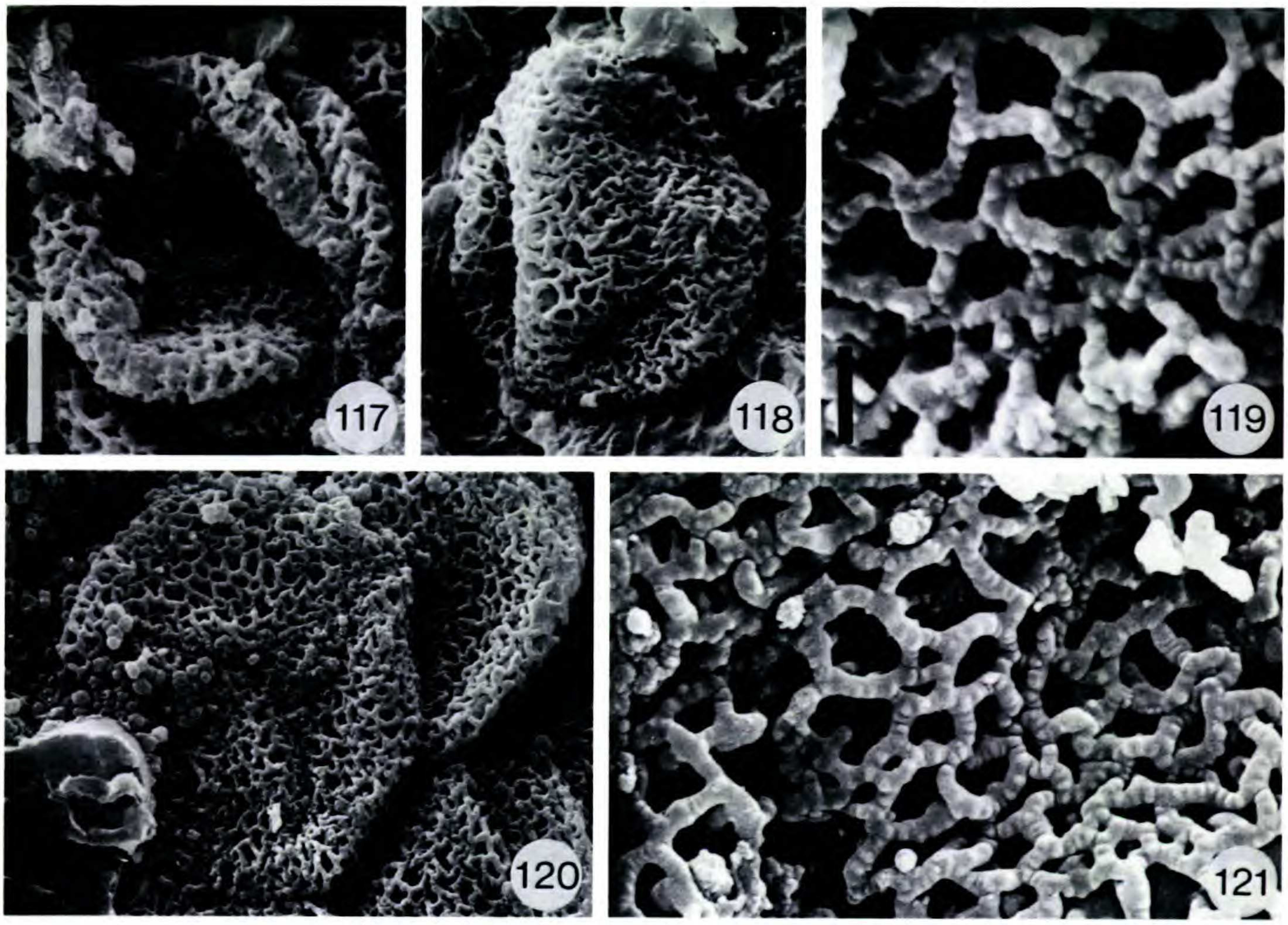
with dense reticulum and broad muri, S105259 (Vale de Agua sample 141). —105. Distal view showing tetrachotomocolpate aperture, ×3000; scale equal to 5 μm. —106. Proximal view, ×3000; scale shown in Figure 105. —107. Detail of reticulum, ×10,000; scale equal to 1 μm. 108–110. Pollen type J.5, monoaperturate (monocolpate to tetrachotomocolpate?) pollen with open reticulum and narrow muri, S105324 (Vale de Agua sample 139). —108. Distal view, ×3000; scale shown in Figure 105. —109. Proximal view, ×3000; scale shown in Figure 105. —110. Detail of reticulum, ×10,000; scale shown in Figure 107. 111–113. Pollen type J.6, Monoaperturate pollen with irregular aperture, open reticulum, and narrow muri, S105659 (Vale de Agua sample 139). —111. Distal view, ×3,000; scale shown in Figure 105. —112. Proximal view, ×3000; scale shown in Figure 105. —113. Detail of reticulum, ×10,000; scale shown in Figure 107. 114–116. Pollen type J.7, monocolpate pollen with open reticulum and narrow muri, S105322 (Vale de Agua sample 139). —114. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 105. —115. Proximal view, ×3000; scale shown in Figure 105. —116. Detail of reticulum, ×10,000; scale shown in Figure 107.



Figures 117–121. Scanning electron micrographs of pollen types J.8 and J.9 from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25) western Portugal. 117–119. Pollen type J.8, trichotomocolpate pollen with open reticulum and narrow muri, S105176. —117. Distal view showing trichotomocolpate aperture, ×3000; scale equal to 5 μm. —118. Proximal view, ×3000; scale shown in Figure 117. —119. Detail of reticulum, ×10,000; scale equal to 1 μm. 120–121. Pollen type J.9, trichotomocolpate pollen with open reticulum and narrow muri, S101222. —120. Distal view showing distinct trichotomocolpate aperture, ×3000; scale shown in Figure 117. —121. Detail of reticulum, ×10,000; scale shown in Figure 119.

and similar grains have also been observed on the surface of a fruit in the same flora.

J.7. Monocolpate pollen with open reticulum and narrow muri (Figs. 114–116). Pollen grains circular in equatorial outline and about 12–13 μm in diameter (Figs. 114, 115). Aperture is monocolpate with a long colpus that reaches to the equator. Aperture margin is distinct, but the membrane has not been observed in any of the specimens. The tectum is open reticulate with lumina of two sizes. Larger lumina are up to 1.4 μm in diameter, and smaller lumina are about 0.25 μm in diameter. Muri are narrow and low, with a rounded profile, about 0.2 μm wide. They are ornamented by faintly developed protrusions. Columellae are long and widely spaced (Fig. 116).

The pollen grains were found in a fragmentary stamen from the Vale de Agua flora.

J.8. Trichotomocolpate pollen with open reticulum and narrow muri (Figs. 117–119). Pollen grains almost circular in outline, about 13 μm in diameter, with a trichotomocolpate aperture (Figs. 117, 118). Arms of the aperture short and broad. Reticulum is open and heterogeneous with lumina ranging in size from about 0.2 μm to 1.2 μm in diameter. Muri are narrow, about 0.3 μm wide, with a rounded profile. They are ornamented by one row of small blunt to spiny protrusions. Columellae are high and relatively densely spaced (Fig. 119).

This pollen type was found in dispersed tetrasporangiate anthers from the Famalicão flora. The anther is about 0.8 mm long and 0.35 mm broad with little sterile tissue between the pollen sacs.

J.9. Trichotomocolpate pollen with open reticulum and narrow muri (Figs. 120, 121). Pollen grains almost circular in outline, about 15 μm in diameter (Fig. 120). Aperture is distinct and trichotomocolpate in most specimens showing the aperture, but monocolpate specimens are apparently also present. Reticulum is heterogeneous with smaller lumina about 0.1 μm and larger lumina up to about 0.6 μm. Muri are narrow, about 0. 3 μm broad, rounded in cross section. They are ornamented by one row of small rounded to spiny processes. Col-

umellae are high and widely spaced (Fig. 121). Ultrastructural study of the pollen wall shows that the endexine is thick and granular under the aperture, but lacking or extremely thin in non-apertural regions (Pedersen et al., 1994a).

This pollen type was found in dispersed anthers from the Famalicão flora. The pollen grains are very similar to those described above (pollen type J.8), but they are slightly larger and have more widely spaced columellae.

The pollen grains from Famalicão are comparable to dispersed grains reported from the Barremian to early Albian of Egypt as "Trichoto-Beatle" (Penny, 1991). They also show some resemblance to slightly larger grains described from the Barremian of southern England as "CfA Retichot-*baccat*" (Hughes, 1994).

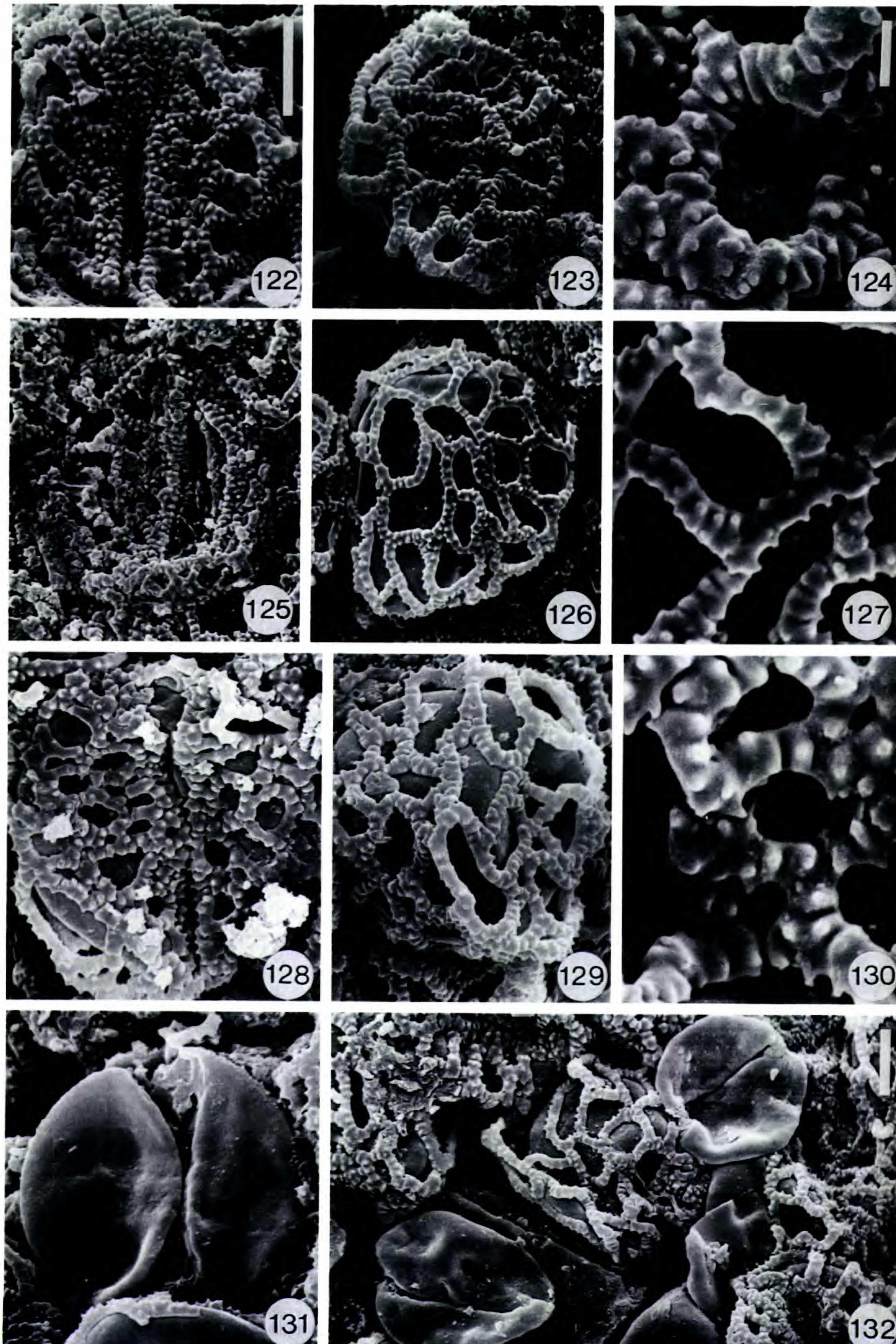
J.10. Monoaperturate pollen with a round aperture, dense reticulum, and broad muri. Pollen grains elliptical in equatorial outline and about 16 μm in diameter. Aperture margin and aperture membrane not exposed. Tectum reticulate with lumina of various sizes. Muri are low, with rounded profile, about 0.3 μm wide. They are ornamented with low blunt processes that are often arranged in two rows. Columellae are of medium size and widely spaced.

The pollen is poorly preserved and not illustrated here. It occurs in a small anther with resin bodies from the Torres Vedras flora. It is very similar to pollen grains associated with fruits of *Couperites mauldinensis* Pedersen, Crane, Drinnan & Friis described from the early Cenomanian of Maryland, U.S.A. (Pedersen et al., 1991) and to dispersed pollen grains assigned to the genus *Clavatipollenites*. Similar pollen was reported from the Barremian of southern England as "Reticulc-monbac" (e.g., Hughes, 1994).

K. Monoaperturate, semitectate, acolumellate, and reticulate pollen with spinulate muri (Figs. 122–132). Pollen grains of this very distinctive type lack columellae and have a very coarse and loosely attached reticulum. They occur abundantly in one sample from the Vale de Agua locality where they are found within stamens and adhering to many specimens of one particular type of fruit. They also occur in many coprolites where they are apparently the only constituents (Figs. 131, 132). Material from this Vale de Agua sample is generally of poor preservation, but some of the anthers are sufficiently well preserved to show the tetrasporangiate organization and the presence of an apical extension of the connective. The stamens differ in size and shape and include pollen grains that differ from each other in details of muri ornamentation and lumen size. Three different species have been distinguished so far. A cluster of dispersed stamens with similar pollen has also been recovered from the early Cenomanian Elk Neck Beds near Mauldin Mountain in northern Maryland, U.S.A. (Crane & Herendeen, 1996). These stamens are also tetrasporangiate with a short apical connective and a very short filament.

Closely similar dispersed pollen grains have been reported from many localities in Europe, Africa, and North America and are sometimes very abundant (Penny, 1988). They range from the Barremian through to the Cenomanian and perhaps to the Turonian (Penny, 1988). The Barremian record from southern England includes pollen with scattered columellae, while the younger records are all acolumellate. They are particularly prominent in Early Cretaceous palynofloras from Egypt and are also common in the Early Cretaceous of North America. From Egypt, 13 different taxa were distinguished from the Mersa Matruh borehole, ranging in age from the earliest Aptian to the Early Albian (Penny, 1988). In these Egyptian samples pollen grains of this type attained their maximum abundance and diversity in the Aptian. The acolumellate taxa from the Mersa Matruh borehole are assigned to the Genusbox "RETIMONO," and different biorecords are distinguished based on pollen size, lumen size and distribution, muri configuration, and supratectal ornamentation. Pollen of this distinctive complex was first described from dispersed grains observed in the Potomac Group sequence and assigned to the genus *Peromonolites* Couper, a dispersed genus established for pteridophyte spores. Two species were recognized, *P. peroreticulatus* Brenner and *P. reticulatus* Brenner (Brenner, 1963). Subsequently both were transferred to the genus *Retimonocolpites* by Doyle et al. (1975) and later to the genus *Brenneripollis* Juhász & Góczán (Juhász & Góczán, 1985). The type species of both *Retimonocolpites* and *Brenneripollis* are different from the acolumellate pollen described here, and Penny (1988) pointed out that neither of these genera are appropriate for this pollen type. Although Doyle (1992) later argued that the holotype of *Brenneripollis*, which was studied using LM only, was perhaps also acolumellate, we follow Penny and exclude the *peroreticulatus* and *reticulatus* species from *Brenneripollis*.

TEM studies of ultrathin sections of the pollen wall of the Portuguese specimens show that although the grains are acolumellate, there is a thin finely granular infratectal layer at the base of the muri. The ektexine is otherwise thick with a thick foot layer and high muri of the tectum. The inner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darker staining layer is very thin in non-apertural regions, but thick under the aperture (work in progress).

K.1. Monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by two to three rows of spinules (Figs. 122–124). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 14–17 μm in diameter (Figs. 122, 123). Colpus is long, reaching to the equator, and has a distinct solid margin with spinules. The tectum is reticulate with a coarse and loosely attached reticulum. Lumina are irregularly rounded, up to about 3 μm in diameter, and of more or less equal size. Small lumina are absent except along the colpus margin where they become very small. Muri are relatively broad, about 1.2 μm wide, and have a flattened and rounded profile. Muri are ornamented by indistinct transverse ridges with distinct spinules that are irregularly aligned in two to three rows (Fig. 124). The spinules tend to extend down the sides of the muri. There are no columellae, except perhaps for single isolated columellae (Fig. 124).

The pollen grains were found in situ in a fragmentary stamen, about 0.4 mm long and 0.32 mm wide, with a tetrasporangiate anther. This species differs from the two other species from the Vale de Agua flora mainly in having broader muri and more than two rows of spinules.

K.2. Monocolpate, acolumellate, and reticulate pollen with narrow muri ornamented by two rows of spinules (Figs. 125–127). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 12.5–15 μm in diameter (Figs. 125, 126). Colpus is long, reaching to the equator, and has a solid narrow margin with spinules. Tectum consists of a coarse and loosely attached reticulum. Lumina are irregular, angular to rounded, varying in size. Small lumina are absent except along the colpus margin. The largest lumina are up to about 5 μm in diameter. Toward the colpus margin the lumina become gradually smaller. Muri are narrow, about 0.6 μm wide, and have a flattened and rounded profile. They are ornamented by transverse ridges with distinct spinules that are typically arranged in pairs and aligned in two rows along the margins of the muri (Fig. 127). There are apparently no columellae.

The pollen grains were found in situ in a fragmentary anther, about 0.5 mm long and 0.15 mm broad, consisting of two elongated pollen sacs. This species differs from the two other species in the Vale de Agua flora mainly in the narrower muri and the two regular rows of spinules.

K.3. Monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by one or two rows of spinules (Figs. 128–130). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 15–19 μm in diameter (Figs. 128, 129). Colpus is long, reaching to the equator, and has a distinct solid margin. The tectum is reticulate with a coarse and loosely attached reticulum. Lumina are irregular, angular to rounded in shape, and of various sizes with small lumina scattered on the proximal surface of the grain. Larger lumina are up to about 5 μm in diameter. Toward the colpus margin the lumina become very small. Muri have a flattened and rounded profile and are about 0.9 μm wide. They are ornamented by irregular transverse ridges and distinct, rather stout spinules that are typically arranged in two longitudinal rows along the margins of the muri. More rarely the spinules are arranged in a single row (Fig. 130). There are apparently no columellae.

The pollen grains were found in situ in small stamens about 0.45 mm long and 0.25 mm broad consisting of a tetrasporangiate anther bearing a short apical extension of the connective. This pollen type is mainly distinguished from pollen type K.1 and K.2 from the Vale de Agua flora in having

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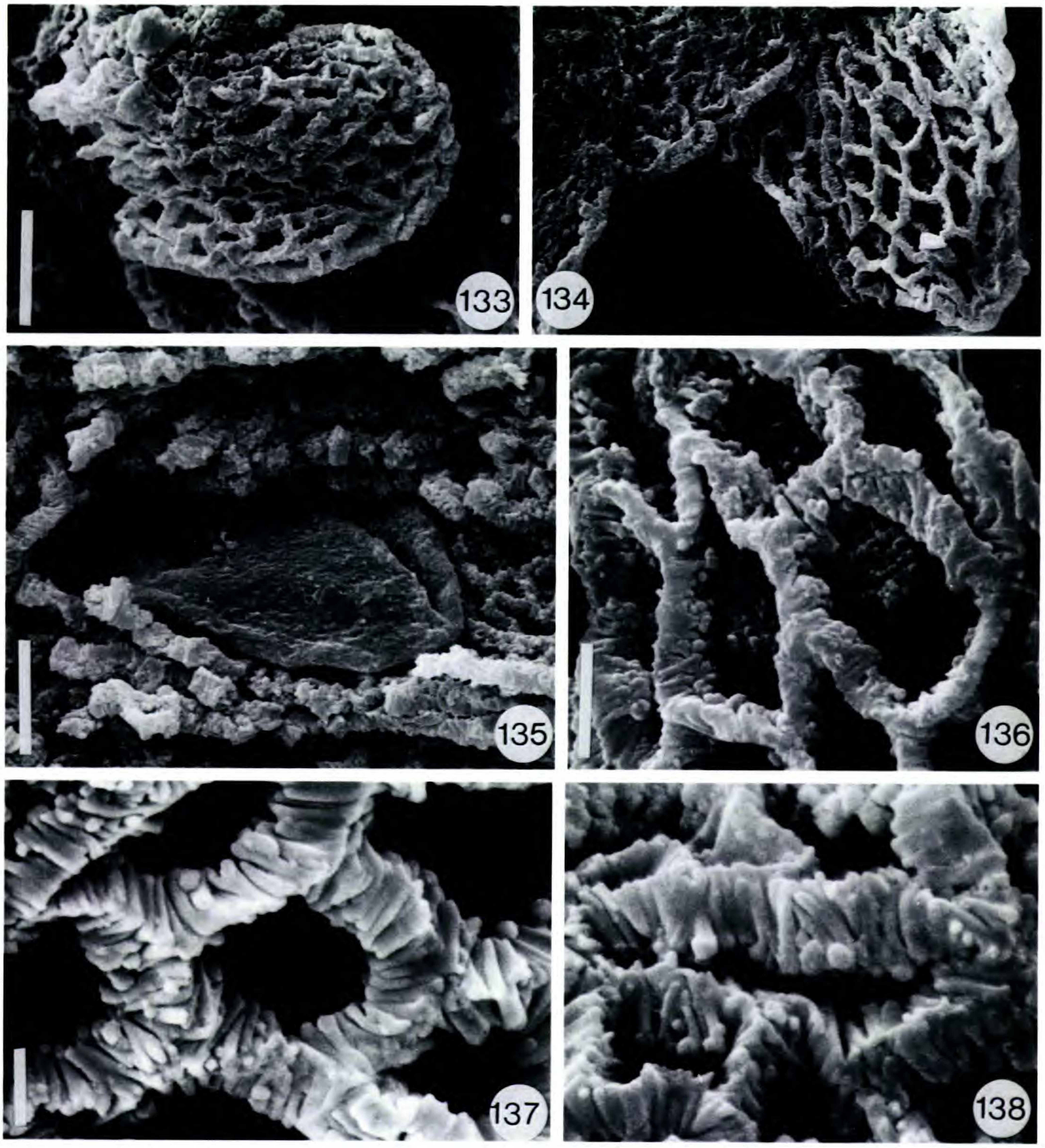
Figures 122–132. Scanning electron micrographs of pollen type K from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 139), western Portugal. 122–124. Pollen type K.1, monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by two to three rows of spinules, S105319. —122. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —123. Proximal view, ×3000; scale shown in Figure 122. —124. Detail of reticulum (with a single columella?), ×10,000; scale equal to 1 μm. 125–127. Pollen type K.2, monocolpate, acolumellate, and reticulate pollen with narrow muri ornamented by two rows of spinules, S105323. —125. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 122. —126. Proximal view, ×3,000; scale shown in Figure 122. —127. Detail of reticulum, ×10,000; scale shown in Figure 124. 128–130. Pollen type K.3, monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by one to two rows of spinules, S105320. —128. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 122. —129. Proximal view, ×3000; scale shown in Figure 122. —130. Detail of reticulum, ×10,000; scale shown in Figure 124. 131–132. Acolumellate pollen of type K.2 from coprolite specimens. —131. Distal view of pollen grain from which the reticulum has been lost, S105327, ×3000; scale shown in Figure 122. —132. Several pollen grains, some from which the reticulum has been lost, S105328, ×2000; scale equal to 5 μm.



Figures 133–138. Scanning electron micrographs of pollen type L from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. Inaperturate (?), acolumellate, and reticulate pollen with segmented muri (*Afropollis*). —133. Single pollen grain showing reticulum, S105253, ×1500; scale equal to 10 μm. —134. Pollen grain showing reticulum and central body, S105250, ×1500; scale shown in Figure 133. —135. Detail of body of pollen grain with reticulum missing, S105250, ×3000; scale equal to 5 μm. —136. Detail of reticulum showing segmented muri and granules, S105250, ×6000; scale equal to 2.5 μm. —137. Detail of reticulum showing segmented muri and granules, S105253, ×10,000; scale equal to 1 μm. —138. Detail of reticulum showing segmented muri and granules, S105253, ×10,000; scale shown in Figure 137.

small lumina scattered on the proximal surface of the grain. In the two other types small lumina only occur on the distal surface close to the colpus margin.

Coprolites with acolumellate and reticulate pollen (Figs. 131, 132). Several small coprolites, about 0.5–1.5 mm long, consisting exclusively of acolumellate pollen of the same type as described above, have been recovered in the same Vale de Agua sample. In some pollen grains the reticulum is lost exposing the psilate foot layer (Figs. 131, 132). In these naked specimens the colpus is distinct and extends to the equator. At least some of the coprolites appear to include only a single pollen type.

The coprolite illustrated in Figures 131 and 132 contains pollen similar to pollen type K.2.

L. Inaperturate (?), acolumellate, and reticulate pollen with segmented muri (Afropollis-type) (Figs. 133–138). Pollen grains of this unique and distinct type lack columellae; they have an open, loosely attached reticulum that is typically free from the much smaller central body and characteristically segmented muri. They are observed in the Vale de Agua flora and are similar to dispersed pollen assigned to the genus *Afropollis* Doyle, Jardiné & Doerenkamp. This genus was established by Doyle et al. (1982) based on pollen grains from the Albian of Peru first assigned by Brenner (1968) to the spore genus *Reticulatasporites* Leschik. *Afropollis* is widespread in Early to mid-Cretaceous strata and is particularly common at low palaeolatitudes in Africa and South America (e.g., Doyle et al., 1982; Penny, 1989, 1991). It is also reported from North America and Europe, with the earliest record in the late Barremian (e.g., Doyle et al., 1982; Penny, 1989). Aperture configuration varies from inaperturate to possibly monocolpate (cryptoaperturate) and zonacolpate, with a ring-furrow that is either displaced toward one pole or is in a symmetrical position dividing the grains in two equal halves (Doyle et al., 1982; Penny, 1989). A winteraceous affinity for the *Afropollis* grains was suggested by Doyle et al. (1990a, 1990b), but in Portugal they occur in separate pollen sacs that are unlike those of extant Winteraceae or any other angiosperms. The structure of the pollen wall is also unlike that in Winteraceae, and currently the systematic affinity of this unique pollen type is unresolved. The presence of a thick endexine may even indicate a non-angiospermous affinity for these grains, but similar segmented muri do occur in some monocotyledonous pollen (e.g., Takahashi, 1982; Le Thomas et al., 1996), and pollen with segmented muri supported by a granular intratectal layer was described for the Liliaceae genus *Erythronium* L. (Takahashi, 1987).

The in situ pollen grains from Portugal are elliptical in outline, about 33 μm in maximum diameter (Fig. 133). No aperture has been observed in the reticulum. The tectum is reticulate with a coarse and open reticulum that is detached from the central body of the grain. The central body known from TEM studies to consist of the foot layer and endexine is much smaller than the reticulum and is about 15–20 μm in diameter (Figs. 134, 135). Lumina are angular and of more or less the same size, up to about 5 μm in diameter. Muri are high, with a triangular profile, about 1 μm wide, and are distinctly segmented transversely. At the base of the muri the segmented part grades into small spherules or granules (Figs. 136–138). TEM sections of the pollen wall show that the wall of the central body consists mainly of a thick endexine, lined by an extremely thin foot layer. A similar wall structure was also shown by Doyle et al. (1990a).

The pollen grains have been found in two separate pollen sacs from the Vale de Agua flora. The pollen sacs are strongly compressed with few details preserved, but unlike other fragments of angiosperm anthers/stamens the pollen sacs are unusual in occurring singly, and may not be angiospermous.

The Portuguese pollen particularly resembles the Egyptian biorecords "Afropol-lumps" from the late Barremian-late Aptian (Penny, 1989, 1991) and "Afropol-jard" from the early Aptian-early Albian (Penny, 1991).

Discussion

The preliminary study of the Torres Vedras, Catefica, Vale de Agua, Famalicão, and Buarcos fossil mesofloras presented here documents an unexpected diversity of angiosperms for this early stage in the evolution of the group. It also documents that in these well-preserved fossil assemblages the number of angiosperm taxa represented by reproductive organs preserved as mesofossils greatly exceeds that previously recognized at other localities of comparable age. In terms of simple species numbers some of the Early Cretaceous floras (e.g., Famalicão, Vale de Agua, and Buarcos) show a level of angiosperm diversity that is comparable to that of rich Tertiary localities. The results presented here also show that there is marked local variation in diversity and abundance of angiosperms among the five floras examined. Even for assemblages collected only a short distance from each other at the same locality, and in the same sedimentary horizon, there is great variation in the abundance and diversity of angiosperms.

Recognition and representation of angiosperms in Early Cretaceous mesofloras and palynofloras from Portugal

In the fossil assemblage from the Famalicão locality there is a very distinct discrepancy between the diversity of angiosperm floral organs recovered and the diversity of angiosperms assessed from dispersed pollen, or from pollen associated with angiosperm reproductive structures. Currently, 105 different taxa based on angiosperm flowers, fruits, and seeds have been identified from the Famalicão

flora. Dispersed stamens have not been included in the counts. Our estimate of 105 different taxa is a minimal estimate, and when possible we have tried to avoid counting different organs of the same species twice. Compared to other localities (e.g., Vale de Agua) there are remarkably few dispersed anthers and very few pollen grains in situ in flowers, or adhering to fruits or stigmatic surfaces. In total 13 different pollen types have been identified in situ from the Famalicão flora. Two are tricolpate, while nine are monoaperturate (monocolpate or trichotomocolpate). One is dicolpate, and one is periporate. Standard palynological preparation of the plant-bearing clay at the Famalicão locality for light microscopy yielded no dispersed angiosperm pollen or other palynomorphs. The paucity of angiosperm pollen in situ in the Famalicão flora may perhaps be explained by the fact that most fossils are charcoalified rather than lignitized, resulting in a lower fossilization potential for pollen. The lack of dispersed pollen in the Famalicão samples may also be explained by differential preservation of organs perhaps in combination with low dispersal of angiosperm pollen to the depositional environment.

The Vale de Agua flora, obtained from several samples collected from the same sedimentary sequence in a large complex of clay pits, has many lignitic fossils and also has the most diverse in situ pollen assemblage of all the Portuguese floras studied so far. Light microscopy of standard palynological preparations revealed only three species of dispersed angiospermous pollen in a palynoflora of about 100 different palynomorph taxa (C. Konradsen, pers. comm., 1997), but currently 26 different angiosperm pollen types have been observed in situ in flowers and dispersed stamens, or on the surface of fruits. Of these, 22 are monoaperturate, one is dicolpate, and three are tricolpate. Many species of flowers, fruits, and seeds occur commonly and consistently in all the various samples, but superimposed on this basic uniformity there is also considerable variation in abundance, diversity, and preservation of the angiosperm reproductive organs. From some samples we have recovered less than one hundred specimens, while from others we have recovered several thousand. Some taxa have been encountered in one sample only. For example, Vale de Agua sample 19 is rich in reproductive organs, but rather poor in in situ angiosperm pollen (5 different types: 4 monocolpate, 1 tricolpate), while Vale de Agua sample 141 includes the most diverse assemblage of in situ pollen that we have encountered (15 different types: 13 monoaperturate, 2 tricolpate). Vale de Agua sample 139 exhibits further variation and has only rare and mostly poorly preserved reproductive organs. However, in this sample stamens are generally better preserved, and 10 different pollen types are known in situ (9 monoaperturate, 1 tricolpate).

Among the pollen types at the Vale de Agua locality (sample 139) are a variety of characteristic semitectate, reticulate, and acolumellate pollen grains (pollen type K). These grains occur in stamens and abundantly on one kind of fruit. They are also the only component in many small coprolites. The plants producing these pollen grains were probably common in the local vegetation, but so far this pollen type has not been encountered in situ in other samples from the Vale de Agua locality. Pollen grains of this type are also absent from the dispersed palynofloras at the Vale de Agua locality. Similar local variation in floristic composition is shown by samples from the Torres Vedras locality. Samples collected in a lignitic horizon in the lower part of the sequence include several monoaperturate pollen types in situ. However, a sample (Torres Vedras sample 144) collected 25 m to the east in the same lignitic horizon yielded several in situ tricolpate forms, not observed in other samples from the same locality.

Like the Famalicão flora, the Buarcos flora is also rich and includes almost 100 different types of angiosperm flowers, fruits, and seeds. There is also a very distinct discrepancy between the diversity of angiosperm reproductive structures and the diversity of pollen associated with the floral organs and the dispersed pollen. Seven angiosperm pollen types have been recorded in the mesoflora (all monoaperturate), and the dispersed palynoflora from the same site studied using light microscopy by Pais and Reyre (1981) is dominated by a variety of fern spores and conifer pollen. Angiosperm pollen is rare and only two taxa were recorded, *Clavatipollenites* cf. *hughesii* and *Apiculatisporis vulgaris* Groot & Groot (later transferred to *Asteropollis* by Singh, 1983). One of these (*Asteropollis*-type pollen) has been detected among the in situ pollen types in the Buarcos flora, where it occurs both in dispersed stamens and on the surface of pistillate *Hedyosmum*-like flowers (pollen type J.4). The remaining six in situ pollen types have not yet been recognized in the dispersed pollen flora. The famous leaf flora from Buarcos (Buarcos-para-Tavarede, Saporta, 1894; Teixeira, 1948) is also collected along the old road from Buarcos to Taverede. The age of this flora is also uncertain, and it is perhaps not contemporaneous with the mesoflora. Saporta (1894) described about 18 different species of angiosperms, but according to studies by Teixeira

(1948) the number of angiosperm taxa is lower, perhaps less than 10.

IMPLICATIONS FOR THE BIOLOGY AND ECOLOGY OF EARLY ANGIOSPERMS

The results presented above document conclusively that angiosperms were more diverse in the Early Cretaceous vegetation around the Torres Vedras, Catefica, Vale de Agua, Famalicão, and Buarcos localities than is indicated by standard LM studies of dispersed palynofloras from those sites. Standard palynological approaches thus provide only a minimum estimate of angiosperm diversity, which may need to be modified based on studies of mesofossils or SEM investigations of dispersed palynofloras (e.g., Penny, 1988; Hughes & McDougall, 1990; Hughes et al., 1991; Penny, 1991; Hughes, 1994). In particular, results from the Portuguese localities suggest that standard palynological studies of the earliest phases of the angiosperm radiation are likely to seriously underestimate both the abundance and diversity of the group. Growth habit and pollination biology of the early angiosperms may have been important factors in the low content of angiosperm pollen in the Early Cretaceous palynofloras. It is interesting that of the 54 pollen types recognized here only *Asteropollis*-type pollen is found in all five Portuguese floras. *Asteropollis*-type pollen also occurs in stamens that have little connective tissue, produced large quantities of pollen, and have elongate pollen sacs that dehisced by simple longitudinal slits. These are all features associated with wind pollination among extant taxa. In addition, *Asteropollis*-type pollen and the floral organs associated with the pollen are closely comparable to extant *Hedyosmum*, which is wind pollinated (Endress, 1987).

The plants that produced the *Asteropollis*-type pollen appear to have been the exception, rather than the rule, in the five floras surveyed here. For example, acolumellate pollen (pollen type K) and most other in situ pollen types are more sporadic in their occurrence in the Portuguese samples. These acolumellate pollen are found in anthers that have an apical expansion of the connective, produced small quantities of pollen, and have small pollen sacs. These are all features that indicate that the plants may have been insect pollinated (Endress, 1996). In addition, there is direct evidence of interaction with insects because these pollen grains occur abundantly in presumed insect coprolites, where they are typically the only component preserved. Many other stamens in the Portuguese floras have similar features indicating insect pollination and low pollen production. Under these circumstances the pollen of this type may not have reached the sedimentary basins in any substantial quantities and will thus require intensive search to detect by standard palynological techniques.

The contrast between the high diversity of angiosperms recognized from mesofossils and low diversity of angiosperms recognized based on dispersed pollen is consistent with the widely accepted hypothesis that most early angiosperms were insect pollinated. In addition, the abundance of angiosperm mesofossils in the Portuguese floras suggests that these plants were a significant component of Early Cretaceous vegetation near the site of deposition. The preservation of delicate structures (e.g., flowers) also suggests minimal transport and implies that the source vegetation was nearby, but as in many other mid-Cretaceous mesofloras angiosperm wood has not been detected, and fragments of angiosperm leaves are rare. Together with the uniformly small size of all the flowers and fruits recovered, these observations suggest that angiosperms represented in the Portuguese floras were of low stature, perhaps small shrubs and herbs. One possible contemporaneous leaf flora from Portugal with angiosperm leaf remains is the flora "Buarcos-para-Tavarede" (Saporta, 1894; Teixeira, 1948), which includes about 10 different angiosperm taxa (Teixeira, 1948), and several of these fossil leaves also have a herbaceous appearance (e.g., *Braseniopsis venulosa* Saporta, *Adoxia praeatavia* Saporta). The Cercal flora, which is probably slightly older, includes 3 angiosperm taxa, all with an herbaceous appearance (*Dicotylophyllum ceriforme* Saporta, *Hydrocotylephyllum lusitanicum* Teixeira, *Nymphaeites choffatii* (Saporta) Teixeira (Teixeira, 1948)). Our results are consistent with the hypothesis advanced by Stebbins (1965) that the earliest angiosperms were perhaps woody shrubs or subshrubs rather than large trees. They are also consistent with evidence from recent phylogenetic analyses of extant angiosperms suggesting that the herbaceous habit was perhaps basal in angiosperms (Taylor & Hickey, 1992; Chase et al., 1993; Qiu et al., 1993). The systematic position of most of the fossil flowers, fruits, and seeds from the Portuguese floras remains to be investigated in detail, but 44 of the 54 pollen taxa identified are of magnoliid or possible monocotyledonous affinity. Among the magnoliids the few taxa for which systematic affinities can be accurately determined have been related to modern families or orders including herbaceous forms (Piperales, Chloranthaceae).

Conclusions

The discovery and description of mesofossil floras containing well-preserved angiosperm flowers, stamens, fruits, seeds, and other reproductive structures from the Late Cretaceous has stimulated a major advance in our current understanding of large-scale patterns in angiosperm evolution (Crane et al., 1995). As these techniques are now applied to a greater range of Early Cretaceous floras, an unexpected diversity of fossil angiosperms is beginning to emerge. In particular, the five mesofossil floras from the Early Cretaceous of Portugal treated in this paper include more than 100 taxa of angiosperm reproductive organs and document the presence of 48 different pollen types with systematic affinities either to extant plants at the magnoliid grade or monocotyledons. A further 10 species referable to the eudicots will be described in a subsequent paper. The diversity of angiosperms recovered from the Portuguese floras contrasts with indications from standard LM studies of dispersed palynofloras, as well as the scarcity of angiosperm wood and leaves in Barremian-Aptian fossil plant assemblages. These discrepancies may reflect important features of the biology and ecology of early angiosperms, including the widespread occurrence of insect pollination and a herbaceous or shrubby habit during the initial phases of their Early Cretaceous radiation.

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